Human-carnivore coexistence and the responses of spotted hyenas (*Crocuta crocuta*) to anthropogenic activity in Ngorongoro Conservation Area, Tanzania

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1. **Dheer**[1], A., Davidian[1], E., Jacobs[2], M.H., Ndorosa[3], J., Straka[1,4‡], T.M., and Höner[1‡], O.P. (2021). **Emotions and cultural importance predict the acceptance of large carnivore management strategies by Maasai pastoralists**. *Frontiers in Conservation Science*. DOI: 10.3389/fcosc.2021.691975

2. **Dheer**[1,5], A., Davidian[1,5], E., Courtiol[5,6], A., Bailey[5,6], L.D., Wauters[7], J., Naman[5], P., Shayo[8], V., and Höner[1,5], O.P. (2022). **Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas**. *Journal of Animal Ecology*. DOI: 10.1111/1365-2656.13812

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“The hyena's persistence is what makes it catch animals”

(Zambian proverb)

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Declaration of independence

Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me. I also declare that I have not submitted the dissertation in this or any other form to any other institution as a dissertation.

Arjun Dheer

December 26th, 2022

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Summary

Human-wildlife coexistence requires rigorous, interdisciplinary evidence that promotes effective conservation and management actions. Such evidence-based approaches are conducive to coexistence between local communities and conflict-prone wildlife, such as large carnivores. Yet, little is known known about the best path to gaining local community acceptance of large carnivore management strategies, the effects of anthropogenic activity on the persistence of large carnivores, and the way large carnivores interact with Threatened wildlife and local communities.

This dissertation focuses on the applied ecology and conservation of large carnivores in Ngorongoro Conservation Area (NCA), Tanzania, a multi-use protected area where the local Maasai community lives alongside wildlife. The three objectives of this dissertation are to: (i) identify the best predictors of the acceptance of large carnivore management strategies by local community members, (ii) assess the effects of anthropogenic activity on large carnivore fitness and physiology, and (iii) understand how large carnivores interact with Threatened wildlife and local communities in multi-use protected areas.

I use an interdisciplinary approach by combining socio-psychological data from the Maasai community with long-term data on the diet, fitness, and physiology of free-ranging spotted hyenas in the NCA. In **Chapter 2**, I show that emotions towards and the cultural importance of large carnivores (spotted hyenas (*Crocuta crocuta*), lions (*Panthera leo*), and leopards (*Panthera pardus*)) are much stronger predictors of the acceptance of large carnivore management strategies than livestock depredation is. I also show that depredation by large carnivores is a much smaller source of livestock death than disease and drought are. I demonstrate that spotted hyenas are viewed less positively than both lions and leopards are, though invasive strategies are not accepted for all three species. The results demonstrate that conservation practitioners may focus too much on livestock depredation as the main impediment to coexistence; rather, they may need to target the respectful fostering of positive emotions through community engagement, while accounting for how different species are viewed. In **Chapter 3**, I investigate the effect of diurnal pastoralism on fitness and physiology in the Ngorongoro Crater spotted hyena population over a 24-year period by exploiting a natural experiment: two of the Crater’s eight spotted hyena clans were exposed to the pastoralism, while the other six were not. By directly measuring the effects of pastoralism on fitness and physiology, I quantify how an anthropogenic activity affects highly conservation-relevant traits. I found no detectable difference in juvenile recruitment (fitness) nor allostatic load (physiology) between the exposed and unexposed clans, indicating that the pastoralism had no major deleterious effect on the spotted hyenas. These results suggest that exposure to anthropogenic activity may be compatible with the persistence of group-living large carnivores, if spatiotemporal overlap between the species' key behaviors and the activity is limited. Finally, in **Chapter 4**, I use fecal DNA metabarcoding to show that the Ngorongoro Crater spotted hyena population does not regularly consume the black rhinoceros (*Diceros bicornis*), a Critically Endangered species. I also show that spotted hyenas at least occasionally leave the Crater to forage, based on detections of both Maasai giraffe (*Giraffa camelopardalis tippelskirchi*) and domestic animals. Furthermore, I found a positive association between spotted hyena age and the propensity to consume domestic animals, which has implications for conflict mitigation.

This dissertation sheds light on (i) the most important variables to target when seeking to gain local acceptance for large carnivore management strategies, (ii) the effects of anthropogenic activity on the fitness and physiology of large carnivores, and (iii) how large carnivores interact with Threatened wildlife and local communities in multi-use protected areas. Altogether, this dissertation is expected to provide valuable knowledge for the optimization of evidence-based large carnivore conservation and human-carnivore coexistence.

Zusammenfassung

Die Koexistenz von Menschen und Wildtieren erfordert gezielte, interdisziplinäre Evidenz, um effektive Schutz- und Bewirtschaftungsmaßnahmen zu etablieren. Solche evidenzbasierten Ansätze sind von zentraler Bedeutung um die Koexistenz zwischen lokalen Gemeinschaften und zu Konflikten neigenden Wildtieren, wie z. B. Großraubtieren zu verbessern. Es ist jedoch nur wenig darüber bekannt, wie die Akzeptanz der lokalen Bevölkerung für Strategien zur Bewirtschaftung von Großraubtieren am besten erreicht werden kann, welche Auswirkungen anthropogene Aktivitäten auf den Fortbestand von Großraubtieren haben und wie Großraubtiere mit bedrohten Arten und lokalen Gemeinschaften interagieren.

Diese Dissertation konzentriert sich auf die angewandte Ökologie und den Schutz Großraubtiere in der Ngorongoro Conservation Area (NCA), Tansania, eine vielseitig genutzte Landschaft, in dem die lokalen Gemeinschaften von Massai-Hirten neben Wildtieren lebt. Die drei Hauptziele der Dissertation beschäftigen sich mit: (i) der Identifizierung der besten Prädiktoren für die Akzeptanz verschiedener Managementstrategien für Großraubtiere bei Mitgliedern der lokalen Gemeinschaft, (ii) der Bestimmung des Einflusses tageszeitlicher Weidehaltung auf die Fortpflanzungserfolg und Physiologie in Gruppen lebenden Großraubtiere, (iii) verstehen wie Großraubtiere mit bedrohten Arten und lokalen Gemeinschaften in vielseitig genutzten Landschaften interagieren.

In dieser Dissertation verwende ich einen interdisziplinären Ansatz, indem ich sozio-psychologische Daten der Massai-Gemeinschaft mit Langzeitdaten über die Ernährung, Fortpflanzungserfolg und Physiologie von Tüpfelhyänen aus einer freilebenden Population in der NCA kombiniere. In **Kapitel 2** zeige ich, dass die Emotionen gegenüber und die kulturelle Bedeutung von Großraubtieren (Tüpfelhyänen, Löwen (*Panthera leo*) und Leoparden (*Panthera pardus*)) weitaus mehr Einfluss auf die Akzeptanz von Managementmaßnahmen für Großraubtiere haben als es die Gefährdung von Viehbeständen hat. Ich zeige auch, dass die Verluste durch Großraubtiere eine deutlich seltenere Ursache für den Tod von Nutztieren sind als Krankheiten und Dürre. Insgesamt wurden Tüpfelhyänen weniger positiv bewertet als Löwen und Leoparden, obwohl invasive Strategien bei allen drei Arten abgelehnt wurde. Die Ergebnisse zeigen, dass sich Naturschützer möglicherweise zu sehr auf die Viehtötung als Haupthindernis für die Koexistenz konzentrieren; stattdessen wäre es möglicherweise besser sich auf eine

respektvolle Stärkung positiver Emotionen durch das Engagement der Gemeinschaft zu konzentrieren und dabei zu berücksichtigen, wie die verschiedenen Arten von der lokalen Gemeinschaft angesehen werden. In **Kapitel 3** untersuche ich die Auswirkungen der Tagesweidehaltung auf die Rekrutierung von Jungtieren und die allostatische Belastung der Tupfelhyänenpopulation im Ngorongoro-Krater über einen Zeitraum von 24 Jahren, indem ich ein natürliches Experiment nutze: zwei der acht Tupfelhyänen Clans im Krater waren der Weidehaltung ausgesetzt, die anderen sechs nicht. Durch die direkte Messung der Auswirkungen der Weidewirtschaft auf den Fortpflanzungserfolg und die physiologischen Merkmale quantifiziere ich, wie sich eine anthropogene Aktivität auf äußerst naturschutzrelevante Eigenschaften der Tupfelhyänen auswirkt. Ich konnte keinen nachweisbaren Unterschied bei der Rekrutierung von Jungtieren (Fitness) oder der allostatischen Belastung (Physiologie) zwischen den exponierten und den nicht exponierten Clans feststellen. Dies deutet darauf hin, dass die Weidewirtschaft keine wesentlichen nachteiligen Auswirkungen auf die Tüpfelhyänen hatte. Diese Ergebnisse lassen darauf schließen, dass die Exposition gegenüber anthropogenen Aktivitäten mit dem Fortbestand gruppenlebender Großraubtiere vereinbar sein kann, wenn die räumlich-zeitliche Überlappung zwischen den wichtigsten Verhaltensweisen der Art und den anthropogenen Aktivitäten begrenzt ist. In **Kapitel 4** schließlich zeige ich anhand von fäkalen DNA-Metabarkodierungen, dass die Tüpfelhyänenpopulation im Ngorongoro-Krater nicht regelmäßig vom Aussterben bedrohte Arten wie Spitzmaulnashörner (*Diceros bicornis*), fressen. Basierend auf DNA-Nachweisen von Massai-Giraffen (*Giraffa camelopardalis tippelskirchi*) und Haustieren in den Kotproben, zeige ich außerdem, dass Tüpfelhyänen zumindest gelegentlich den Krater zur Nahrungssuche verlassen. Darüber hinaus wurde ein positiver Zusammenhang zwischen dem Alter der Tupfelhyänen und der Neigung zum Verzehr von Haustieren festgestellt, was Hinweise zum für das Konfliktmanagement liefert. Diese Dissertation gibt Aufschluss über (i) die wichtigsten Variablen zur Verbesserung der lokalen Akzeptanz von Managementstrategien für Großraubtiere, (ii) die Auswirkungen anthropogener Aktivitäten auf den Fortpflanzungserfolg und Physiologie von Großraubtieren und (iii) die Art und Weise, wie Großraubtiere mit bedrohten Arten und lokalen Gemeinschaften in vielseitig genutzten Landschaften interagieren. Zusammenfassend sollte diese Dissertation wertvolles Wissen für die Optimierung des evidenzbasierten Großraubtierschutzes und die Koexistenz von lokalen Gemeinschaften und Raubtieren.

Chapter 1

General introduction

The *Anthropocene* is a proposed geological epoch characterized by significant anthropogenic signatures in Earth's ecosystems (Lewis & Maslin, 2014). Among the most salient of these anthropogenic signatures are the effects that humans have on wild animals (Cumming, 2020; Lorimer, 2015). These effects have become stronger over time and are often negative (Dirzo et al., 2014; Gaynor et al., 2018; Voigt & Kingston, 2015), which has led to human-wildlife conflict and challenges to coexistence (Guiden et al., 2020; Linnell et al., 2020; Liu, Yang, & Li, 2016). Identifying the causes, consequences, and mitigators of these effects is of primary research interest in applied ecology and conservation biology, disciplines that foster human-wildlife coexistence in a changing world (Caro et al., 2014; Johnson et al., 2017; Lindsey et al., 2022; Wagner, 2020; Young et al., 2015).

Achieving human-wildlife coexistence is contingent on using scientific evidence to inform management strategies (Cook et al., 2016). This approach, known as 'evidence-based conservation', is frequently touted as the most data-driven, effective, and rigorous way to promote human-wildlife coexistence (Segan et al., 2011; Sutherland et al., 2004; Watson et al., 2016). However, there is a lack of scientific research and evidence related to the human-wildlife nexus across many landscapes of high conservation importance worldwide (Gaston et al., 2008; Watson et al., 2014).

This lack of scientific research and evidence has led to the worsening of human-wildlife conflict, the misallocation of research effort, and the application of inadequate management strategies (Le Saout et al., 2013). For instance, it has been shown that local community acceptance of management strategies is necessary for coexistence and conflict mitigation (Dickman, 2010). Yet, local community perspectives and preferences have been largely excluded from conservation policymaking, even in mixed-use, shared landscapes (Berkes, 2007; Thondhlana et al., 2020). This exclusion and resulting conflict may partly explain why many wildlife populations continue to decline (Barnes et al., 2016; Western, Russell, & Cuthill, 2009). In addition, the effects of anthropogenic activity on wildlife behavior are well-studied (Bond et al., 2021; Doherty et al., 2021), but little is known about how it affects traits that are more conservation-relevant, such as fitness and physiology (Ménard et al., 2014). Consequently, the link between anthropogenic activity and actual wildlife persistence is unclear. Relying on weak evidence to inform management strategies can also have negative consequences for conservation. For example, decisions to cull one species to protect another may be based on unverified reports or rumor (Johnson, Isaac, & Fisher, 2007; Newsome et al., 2017). Such flawed management can have undesirable consequences for competitors or prey. Therefore, it is crucial that conservation and management strategies be based on high-quality evidence to optimize human-wildlife coexistence.

The need to optimize human-wildlife coexistence is particularly urgent for the persistence of large carnivores, a guild of large-bodied (>20 kg mean adult body mass) species of the mammalian order *Carnivora* (Curveira-Santos et al., 2021; Ray et al., 2013). The large carnivore guild includes some of the most charismatic, controversial, culturally important, and emotionally evocative wildlife species on Earth (Braczkowski et al., 2022; Carter & Linnell, 2016; López-Bao, Bruskotter, & Chapron, 2017; Packer et al., 2013). They also provide key ecosystem services as apex predators and scavengers, e.g., by keeping prey populations healthy and limiting the spread of disease (del Rio et al., 2001; Ripple et al., 2014). Currently, over 80% of large carnivore species are experiencing population declines, and 64% are classified as Threatened on the International Union for the Conservation of Nature (IUCN) Red List (Wolf & Ripple, 2018). Accordingly, there is a pressing need for human-carnivore coexistence. Yet, many important questions about them remain unanswered, including the factors that best predict local community acceptance of large carnivore management strategies, the effects of anthropogenic activity on large carnivore fitness and physiology, and interactions between large carnivores, Threatened wildlife, and local communities in mixed-use, shared landscapes (Figure 1).

Figure 1: Examples of large carnivores and nearby anthropogenic signatures. A. A spotted hyena (*Crocuta crocuta*) in proximity to Maasai pastoralists and their cattle in the Ngorongoro Crater, Tanzania (Picture credit: Oliver P. Höner; shared with permission). B. A family of cheetahs (*Acinonyx jubatus)* in proximity to farmland in Lewa Wildlife Conservancy, Kenya (Picture credit: Arjun Dheer).

1.1 Local community acceptance of large carnivore management strategies

To be effective, large carnivore management strategies must be accepted by local communities. A lack of local community acceptance of management strategies may cause conflicts with wildlife and local authorities, creating a 'lose-lose' situation where neither people nor wildlife benefit (Redpath et al., 2013; Treves & Santiago-Ávila, 2020). Therefore, it is important to understand which large carnivore management strategies are most accepted by local communities, the factors that predict their acceptance, and how acceptance varies across species. However, there are limited data on these topics, especially in the Global South, where large carnivores – and the benefits and burdens of living alongside them – are mostly concentrated (van Eeden et al., 2018; Monsarrat & Svenning, 2022). Most research on human-carnivore coexistence focuses on the perspectives of Western, Educated, Industrialized, Rich, and Democratic (WEIRD; Henrich, Heine, & Norenzayan, 2010) people in the Global North (Lozano et al., 2019). Thus, further research on the acceptance of large carnivore management strategies by local communities in the Global South is needed to support human-carnivore coexistence.

1.1.1 Large carnivore management strategies in context

Large carnivore management strategies aim to balance the needs of local communities with those of large carnivores, but these needs can often be in conflict. For instance, large carnivores can regularly attack livestock (Khorozyan et al., 2015), which can be a problem for pastoralist communities, who rely on livestock for food security and other resources (Broekhuis, Cushman, & Elliot, 2017; Manral et al., 2016). At the same time, large carnivores can also pose threats to human safety through defensive or predatory attacks (Bhattarai & Fischer, 2014). Ostensibly, the interests of large carnivores and local communities may be in opposition. However, large carnivores also provide benefits: apart from ecosystem services, they are tourism drawcards and have considerable economic value (Sillero-Zubiri & Laurenson, 2001). Therefore, applying large carnivore management strategies is complex and requires consideration of stakeholder needs.

Large carnivore management strategies can be divided into two groups: ‘invasive’ and ‘protective’. Invasive strategies include aversive conditioning (exposing the animal to unpleasant stimuli), lethal control (killing the animal), relocation (moving the animal), and sterilization (neutering or spaying the animal; van Eeden et al., 2018). These strategies are often used as a last resort in response to attacks on people or livestock by ‘problem animals’ (Linnell et al., 1997). Protective strategies do not harm the animal and include no action (maintaining the status quo), compensation (paying communities for human or livestock death/injury), conservation incentive payments (paying communities for large carnivore presence), and improving livestock corrals (Bauer et al., 2017). Each strategy has its own advantages and disadvantages, and its appropriateness will depend on local customs and laws (Carter & Linnell, 2016). Ultimately, local community acceptance of large carnivore management strategies is essential, but it is unclear what factors best predict acceptance.

1.1.2 Predicting the acceptance of large carnivore management strategies

1.1.2.1 Livestock depredation

Most research on human-carnivore coexistence and large carnivore management strategies has focused on livestock depredation. Livestock depredation is a negative experience that is outside an individual's control, and it is widely considered a major driver of conflict (Miller et al., 2016; Ogada et al., 2003). For example, in response to livestock depredation, local communities may retaliate by killing large carnivores, or protected area staff may cull or relocate them (Ikanda & Packer, 2008; Kissui, 2008; Lute et al., 2018). It is therefore predicted that livestock depredation is positively associated with the acceptance of invasive large carnivore management strategies.

1.1.2.2 Socio-psychological variables

Recently, there has been growing interest in how socio-psychological variables, known as ‘human dimensions’, influence the acceptance of large carnivore management strategies (Jacobs et al., 2018; Manfredo et al., 2021). These variables include the emotions felt towards large carnivores and the cultural importance they hold (Gebresenbet et al., 2018; Sibanda et al., 2020). Past research suggests that these variables likely play a significant role in driving conflict with or tolerance of large carnivores (Krafte Holland, Larson, & Powell, 2018). For example, positive emotions and high cultural importance may be associated with the acceptance of protective management strategies (Frank, 2016; Sponarski, Vaske, & Bath, 2015).

Emotions are linked to affective pathways in the human brain, which are associated with short-term, transient feelings and reactions (Panskepp, 2005). Large carnivores can evoke positive emotions such as happiness because of their aesthetic appeal, rarity, size, and strength (Castillo-Huitrón et al., 2020; Ghasemi et al., 2021). They can also evoke negative emotions such as anger or disgust if perceived as greedy, ugly, or unintelligent (Dickman, Marchini, & Manfredo, 2013). Positive and negative emotions may be strongly associated with the acceptance of protective and invasive management strategies, respectively (Rode et al., 2021). Because emotions change quickly, they can be readily influenced to become more positive or negative (Straka, Greving, & Voigt, 2021).

Cultural importance ratings are linked to cognitive pathways, or the inference of deeply-held, long-term beliefs (Healey & Grossman, 2018). The cultural importance placed on large carnivores can vary widely depending on the species and community involved. In some communities, particular species play symbolic roles in heraldic rituals or religious ceremonies (Schwartz, 2006). They may also be depicted positively in folklore and mythology, which can make them culturally important (Hazzah, Chandra, & Dolrenry, 2019). On the other hand, if they are depicted negatively, they may be considered culturally unimportant (Glickman, 1995). Previous research, though scarce, suggests that cultural importance is associated with tolerance of large carnivores and the acceptance of protective management strategies (Inskip et al., 2016).

Given the suggested strong influence of livestock depredation on management strategy acceptance and the recent findings on the influence of emotions and cultural importance, it is important to compare the predictive potential of all three variables. This will help identify which is the best predictor and inform applied ecologists and local authorities which factors to prioritize when promoting evidence-based large carnivore conservation and human-carnivore coexistence.

1.2 Effects of anthropogenic activity on large carnivore fitness and physiology

A considerable amount of research has documented how anthropogenic activities, which can range from localized practices such as gardening and recreational hiking, to large-scale ones like deforestation and manufacturing, affect wildlife. This research has greatly increased our understanding of how wildlife copes with an increasingly human-dominated world and can be used to develop evidence-based conservation and management strategies (Lewis et al., 2021). For instance, past research suggests that the responses of wildlife to anthropogenic activity may differ greatly based on the type of activity occurring and the social system and biology of the focal species (Tablado & Jenni, 2017). One of the most powerful ways to study this relationship is to use 'natural experiments', where the effects of changes in anthropogenic activity on key traits in wildlife are quantified (Hebblewhite et al., 2005). Such natural experiments can provide rigorous evidence of how anthropogenic activity affects wildlife. Yet, they are difficult to execute in free-ranging populations, especially for long-lived, wide-ranging animals such as large carnivores. Hence, there is a need for natural experiments focused on the effects of anthropogenic activity on large carnivores to aid evidence-based large carnivore conservation and human-carnivore coexistence.

1.2.1 Effects of anthropogenic activity on behavior

Most research on the relationship between anthropogenic activity and large carnivores has focused on changes in behavior, such as activity patterns, diets, habitat use, and movement (Gaynor et al., 2018; Newsome et al., 2014). There is strong evidence that these changes can be substantial – large carnivores usually become more nocturnal, eat more domestic animals or human refuse, and have more fragmented habitats and movement patterns in response to increased anthropogenic activity (Abrahms et al., 2022; Alexander et al., 2016; Wilmers, Nisi, & Ranc, 2021). These effects may be assumed to be detrimental to the species' persistence.

But this is not necessarily the case. Changes to wildlife behavior do not always threaten population persistence and the challenges they pose to conservation may be exaggerated (Iglesias-Carrasco, Wong, & Jennions, 2022; Leblond, Dussault, & Ouellet, 2013). Animals have a degree of plasticity that may allow them to adjust their behavior to handle a modicum of anthropogenic activity (Caspi et al., 2022). And, it is often unknown how far these adjustments can go before they begin to detectably, negatively impact population persistence (Schell et al., 2021). To fully understand how anthropogenic activity affects large carnivore persistence, there is accordingly a need to go deeper and quantify its effects on traits more relevant to conservation, such as fitness and physiology.

1.2.2 Going deeper: effects of anthropogenic activity on fitness and physiology

1.2.2.1 Fitness

Darwinian fitness refers to the ability of an animal to survive and reproduce in a given environment (Metz, Nisbet, & Gertiz, 1992; Sæther & Engen, 2015). Measuring fitness in wildlife is imperative for conservation; it provides insights into how well a population copes with its environment and how it responds to changes therein, e.g., those induced by anthropogenic activity. Fitness is often measured in terms of reproductive performance and survival, which can be integrated into a single metric: recruitment, or the number of individuals added to a population via birth and/or immigration (Chesson, 2003).

By quantifying how anthropogenic activity influences recruitment, applied ecologists and local authorities can monitor the performance of social groups and populations (Gordon, 1988). This type of monitoring is valuable, as it allows ensuing conservation and management strategies to be based on data and evidence, rather than defective assumptions, rumor, or speculation. And, by understanding the effects of anthropogenic activity on recruitment, applied ecologists and local authorities can develop targeted strategies to protect social groups and populations while meeting the needs of local communities.

Despite its great value, studying the relationship between anthropogenic activity and fitness in wildlife is difficult and rarely done. So far, the limited research on this relationship has primarily focused on small, short-lived animals, such as insects (*Insecta* spp.) and rodents (*Rodentia* spp.; Wagner, 2020). Collecting sufficient longitudinal data on free-ranging large carnivore populations to execute such studies requires much more funding, manpower, and time (del Rio et al., 2001). Additionally, it can be challenging to disentangle the effects of anthropogenic activity from those of other key variables, such as the presence of competitors, disease outbreaks, prey abundance, and population size (Ciuti et al., 2012). Nonetheless, if well-executed, such studies can provide insights of critical importance to local authorities who seek to establish human-carnivore coexistence.

1.2.2.2 Physiology

Physiology is the study of how an organism's cells, tissues, and organs work together to maintain life and support development, growth, and reproduction (Birnie-Gauvin et al., 2017). Monitoring physiology is important for conservation because it provides insights into animal health and survival (Madliger et al., 2020). Indeed, physiological changes can have major consequences for population persistence, given that they can substantially affect an individual's ability to survive in a given environment (Wikelski & Cooke, 2006).

Environmental disturbances can result in substantial physiological changes. For example, exposure to pollutants can alter hormone levels, impair immune function, or increase disease risk (Scott & Sloman, 2004). Additionally, changes in weather conditions or food availability can strongly affect an animal's metabolism and ability to maintain a healthy body weight (Boos, Boidot, & Robin, 2005). These environmentally-induced physiological effects can have consequences for individuals and populations, and are thus highly conservation-relevant (Badry et al., 2021).

There is currently a lack of knowledge, however, specific to how anthropogenic activity affects physiology in wildlife. This is, again, particularly true for large carnivores, which may be highly susceptible to experiencing detectable physiological changes due to environmental disturbances (Morales-González et al., 2020; Støen et al., 2015). In order to develop effective conservation and management strategies for large carnivores, it is important to understand how anthropogenic activity affects their physiology. Applied ecologists and local authorities can then implement strategies that allow both local communities and large carnivores to thrive.

1.3 Interactions between large carnivores, Threatened wildlife, and local communities in multi-use protected areas

Approximately 15% of the Earth's land surface is conserved within ‘protected areas’ (PA; Pimm, Jenkins, & Lee, 2018). PA are established to protect habitats and halt or reverse biodiversity loss (Lewis et al., 2019). While the number and extent of PA has increased over time, their effectiveness is often questioned due to issues such as corruption, over-tourism, poaching, inadequate funding, deficient monitoring and evaluation, limited research effort, and insufficient staff (Appleton et al., 2022; Maxwell et al., 2020; Watson et al., 2014). The ethical value of PA has also been questioned because many implement ‘fortress conservation’, which involves displacing local communities for wildlife and tourism (Siurua, 2006). This criticism led to the development of multi-use protected areas (MUPA), where humans and wildlife cohabit (Blackman, 2015). Rigorous data from MUPA are sparse, raising questions about how well they meet the double mandate to protect the interests of both local communities and wildlife (Pekor et al., 2019).

1.3.1 Conservation questions about large carnivores in multi-use protected areas

1.3.1.1 Interactions with Threatened wildlife

Some wildlife species are mostly or entirely restricted to MUPA and other mixed-use conservation landscapes (e.g., northern white rhinoceros (*Ceratotherium simum cottoni*): see Ryder et al., 2020). These species often serve as conservation umbrellas for other wildlife and bring ample funds to MUPA. Local community members residing in or around MUPA may be directly involved with the protection of such species, e.g., as rangers or scouts (Sibanda et al., 2022). This form of stewardship is most often directed towards charismatic megafauna, especially those classified as ‘Endangered’ or ‘Critically Endangered’ (both of which fall under the ‘Threatened’ category on the IUCN Red List; Muntifering et al., 2017; Smith et al., 2016). Accordingly, local communities, authorities, and tourism lodges may synergistically safeguard such species.

However, these combined efforts can sometimes create dilemmas when one priority species is suspected to limit another. For example, Threatened large carnivores may regularly prey on Threatened ungulates (e.g., lions (*Panthera leo*) and Grevy's zebra (*Equus grevyi*): see Davidson et al., 2019). Such cases raise an important question: what to do when one protected species is suspected to prey on another? To answer this question, it is essential to gather the evidence necessary to determine if the large carnivore regularly consumes the focal species, and if so, whether it poses a credible threat to the focal species' persistence in the MUPA. Gathering this evidence is possible through a study of the large carnivore's diet. From there, local authorities can implement management strategies towards evidence-based large carnivore conservation.

1.3.1.2 Diet studies and interactions with local communities

Studies on the diets of large carnivores are well-represented in the scientific literature and have provided seminal understandings of community and trophic ecology (Bojarska & Selva, 2012; Lyngdoh et al., 2014). Researchers can apply several methods to investigate the diets of large carnivores, including camera-mounted collars, direct observations, GPS clusters, morphological analyses, stable isotope analyses, and DNA metabarcoding (Hilderbrand et al., 1996; Jensen et al., 2022; Monterroso et al., 2018; Tezuka et al., 2022; Wachter et al., 2012). Each method has its own set of strengths and limitations, and the most appropriate method will vary according to the specific research questions being asked and the accessibility of different resources.

Traditionally, diet studies often focused on fundamental ecological topics, such as predator-prey interactions, interspecific competition and facilitation, and resource selection (Carvalho & Gomes, 2004; Mukherjee, Goyal, & Chellam, 1994; Hayward, 2006). More recently, there has been added focus on applying findings to provide management recommendations (Janeiro-Otero et al., 2020; Mengüllüoğlu et al., 2018; Shao et al., 2021). Taking an applied approach yields valuable insights into the management of large carnivores and is of broad relevance to applied ecologists, local authorities, and local communities alike.

One such application is the assessment of how large carnivores behave in mixed-use landscapes, including their interactions with local communities. For instance, evidence of the consumption of domestic animals can identify potential conflicts with local communities or beneficial scavenging of dead or diseased livestock (Yirga et al., 2013). Similarly, evidence of the consumption of species that are found only in human-dominated areas can provide information on landscape connectivity and space use in urban, peri-urban, or patchy environments (Athreya et al., 2016). These applications highlight the potential flexibility and value of large carnivore diet assessments, and their usefulness in informing conservation and management decisions.

Diet studies can also be useful to identify how variation in socio-demographic traits can influence a large carnivore’s tendency to consume domestic animals. This may shed light on the propensity of individual large carnivores to conflict with local communities (Bhattacharjee & Parthasarathy, 2013; Linnell et al., 1999). For instance, anecdotal reports suggest that variables such as age, health, and social rank may greatly affect a large carnivore's tendency to attack livestock or be a ‘man-eater’, but this hypothesis is difficult to test (Gupta & Kumar, 2013; Löe & Röskaft, 2004). Again, collecting robust ecological data pertaining to large carnivores can be challenging, due to the need for sufficient sample sizes and the difficulty of monitoring these animals in the wild (Wolfe et al., 2015). This can inhibit conflict mitigation, to the detriment of both local communities and large carnivores.

Potentially, key conservation questions regarding large carnivores in MUPA can be answered through rigorous diet assessments. Such studies may allow applied ecologists and local authorities to obtain data on how large carnivores interact with local communities and Threatened wildlife in mixed-use, shared landscapes. This type of data may be conducive to promoting evidence-based large carnivore conservation and human-carnivore coexistence.

1.4 Aim and objectives

This dissertation aims to promote evidence-based large carnivore conservation and human-carnivore coexistence. It uses an interdisciplinary approach to study human-carnivore interactions and the responses of spotted hyenas (*Crocuta crocuta*) to anthropogenic activity in Ngorongoro Conservation Area (NCA), Tanzania. The research herein combines socio-psychological data from the Maasai community with long-term data on the diet, fitness, and physiology of the free-ranging population of spotted hyenas in the Ngorongoro Crater, a volcanic caldera within the NCA (Figure 2).

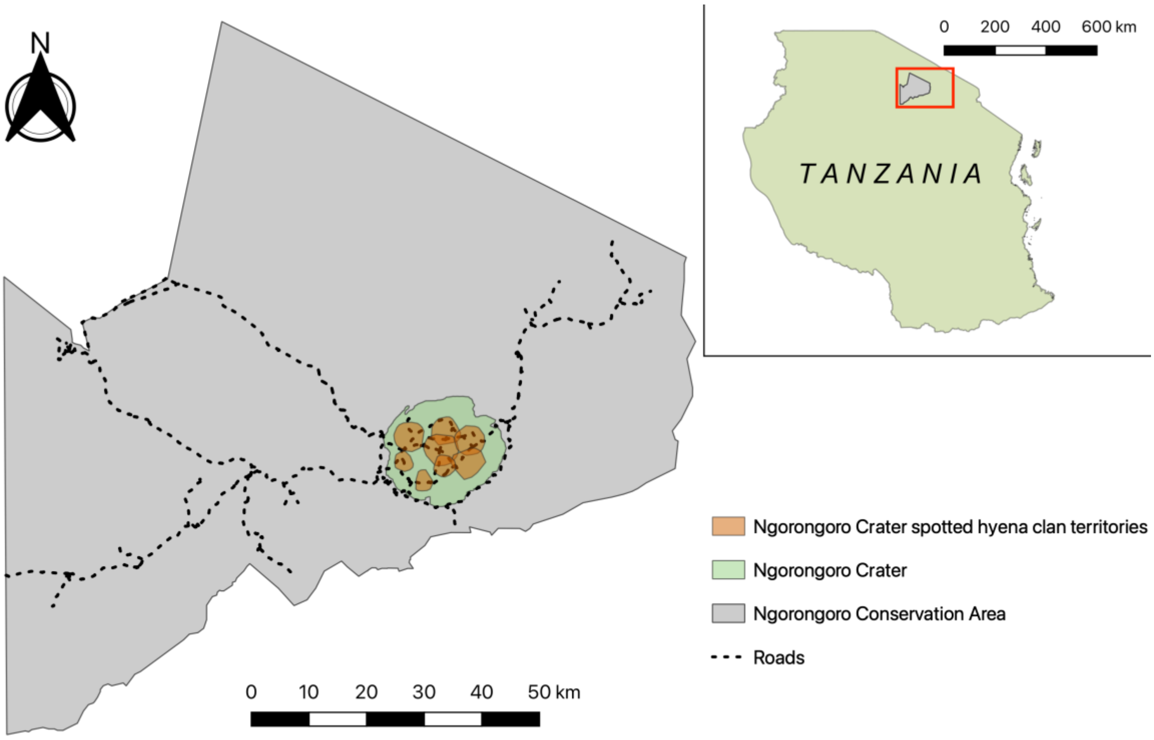

Figure 2: Map of the dissertation study area. Ngorongoro Crater spotted hyena clan territory boundaries are based on 85% minimum convex polygons (MCP) of adult female spotted hyena sightings from 1996-2019 for each clan. MCP of 85% were chosen to accurately represent the locations of clan territories across the study period. The map inset depicts the location of the Ngorongoro Conservation Area, a multi-use protected area in Tanzania. The red rectangle within the inset shows the area of detail in the main map.

The dissertation has three objectives:

- **Identify the best predictors of the acceptance of large carnivore management strategies by local community members.** To achieve this objective, I quantify the predictive potential of emotions, cultural importance, and livestock depredation on the acceptance of three management strategies commonly applied to mitigate human-carnivore conflict: no action, relocation, and lethal control. I use structured, closed questionnaires conducted in collaboration with the local Maasai community and focus on the three largest, most conflict-prone carnivores in sub-Saharan Africa: spotted hyenas, lions, and leopards (*Panthera pardus*).

- **Assess the effects of anthropogenic activity on large carnivore fitness and physiology.** I use a natural experiment to investigate the effects of diurnal pastoralism on juvenile recruitment and allostatic load in spotted hyenas in the Ngorongoro Crater, Tanzania, over a 24-year period. I compare juvenile recruitment in clans exposed and unexposed to pastoralism. I also compare fecal glucocorticoid metabolite concentrations (fGMC) – a biomarker of an organism's allostatic load – between exposed and unexposed clans.

- **Understand how large carnivores interact with Threatened wildlife and local communities in multi-use protected areas.** I use DNA metabarcoding – an emerging molecular tool to assess diet – to understand whether spotted hyenas regularly consume a Critically Endangered species in the Ngorongoro Crater. I also investigate whether spotted hyenas leave the Crater by assessing if they consumed species that are only extant outside. In addition, I estimate their selection for different wildlife species. Finally, I quantify the effects of socio-demographic variables on the propensity of spotted hyenas to consume domestic animals.

I address the three objectives of this dissertation in three chapters:

Chapter 2: Emotions and cultural importance predict the acceptance of large carnivore management strategies by Maasai pastoralists

In this chapter, I compare the predictive potential of emotions, cultural importance, and livestock depredation to determine which is the strongest predictor of large carnivore management strategy acceptance by Maasai pastoralists. I test predictions derived from the hypothesis that management strategy acceptance is influenced by the emotions towards, cultural importance of, and livestock depredation by large carnivores. I focus on three commonly-applied large carnivore management strategies: no action, relocation, and lethal control, and the three largest, most conflict-prone carnivores in sub-Saharan Africa: spotted hyenas, lions, and leopards. I thereby identify which variable is the best predictor of different management strategies, and thus which should be focused on when seeking local acceptance to promote human-carnivore coexistence. I further describe differences in local perceptions towards the three species. Additionally, I assess how the number of livestock deaths attributed to the large carnivores compares to that attributed to disease and drought.

Chapter 3: Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas

In this chapter, I assess how diurnal pastoralism affects juvenile recruitment (fitness) and allostatic load (physiology) of spotted hyena clans over a 24-year period within the Ngorongoro Crater. I use detailed behavioral, physiological, and socio-demographic data from all eight clans to compare the performance of clans exposed and unexposed to the pastoralism. I build on previous findings in the wider literature which thoroughly document how anthropogenic activity can affect wildlife behavior. By going deeper and quantifying effects on fitness and physiology, I determine how anthropogenic activity affects traits more relevant to the conservation and persistence of wildlife. I also describe how the effects of anthropogenic activity on wildlife may differ according to the characteristics of the activity – particularly its predictability and disruptiveness – and the biology and social system of the focal species. I further provide a new perspective on investigating the effects of anthropogenic activity on wildlife by measuring fitness at the level of social groups.

Chapter 4: DNA metabarcoding provides answers to key conservation questions about spotted hyenas

In this chapter, I assess the diet of the Ngorongoro Crater spotted hyena population to answer conservation questions regarding their interactions with Threatened wildlife and the Maasai community in the wider NCA. Using DNA metabarcoding of 371 fecal samples collected over a 24-year period, I determine whether the spotted hyenas regularly consume Critically Endangered black rhinoceros (*Diceros bicornis*), if they forage in pastoralist areas that surrounded the Crater by assessing whether they consume species found exclusively outside the Crater, and if socio-demographic variables strongly influence their propensity to consume domestic animals. I thereby investigate conservation dilemmas that can occur if one protected species is suspected to limit another, large carnivore behavior in MUPA, and the influence of socio-demographic variables on the propensity of individual large carnivores to consume domestic animals.

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Chapter 2

Emotions and cultural importance predict the acceptance of large carnivore management strategies by Maasai pastoralists

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Detailed contributions:

The original idea to compare the predictive potential of different variables on management strategy acceptance was developed by Tanja Straka (TS) and Maarten Jacobs (MJ). The idea to embed the study with the Ngorongoro Conservation Area Maasai community and large carnivore guild was implemented by Arjun Dheer (AD), TS, and Oliver Höner (OH). Community engagement and the conduction of questionnaires was done by AD and Julius Ndorosa (JN). Data curation was handled by AD and JN. Statistical analyses were conceptualized and conducted by AD, Eve Davidian (ED), and Alexandre Courtiol, under the guidance of OH and TS. The manuscript was primarily written by AD and TS, and edited by ED, MJ, and OH.

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Emotions and Cultural Importance Predict the Acceptance of Large Carnivore Management Strategies by Maasai Pastoralists

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Management strategies to reduce human-carnivore conflict are most effective when accepted by local communities. Previous studies have suggested that the acceptance depends on emotions toward carnivores, the cultural importance of carnivores, and livestock depredation, and that it may vary depending on the types of strategies and carnivores involved. However, no study so far considered these factors simultaneously to compare their influence on the acceptance of management strategies. We quantified the predictive potential of these factors on the acceptance of three management strategies frequently applied to mitigate human-carnivore conflict: no action, relocation, and lethal control. We interviewed 100 members of the Maasai community in Ngorongoro Conservation Area in Tanzania. We used structured, closed questionnaires and focused on the three large carnivores involved in the most depredation regionally: spotted hyenas (*Crocuta crocuta*), lions (*Panthera leo*), and leopards (*Panthera pardus*). We found that the majority of respondents accepted no action and rejected relocation and lethal control for all three carnivores. The acceptance of the management strategies was strongly influenced by the emotion joy and by the cultural importance of carnivores, and the effects of joy and cultural importance were stronger than the effect of livestock depredation. We conclude that authorities should evaluate the emotions and cultural importance that local communities associate with carnivores when seeking to gain acceptance of management strategies and account for differences between species. Finally, we recommend that future human-carnivore coexistence studies should consider the socio-psychology of local communities and be done longitudinally to detect shifts in cultural, emotional, and ecological factors over time.

Keywords: large carnivores, emotions, human dimensions, livestock depredation, human-wildlife conflict, non-weird people, culture, pastoralism

INTRODUCTION

Local communities play a crucial role in conservation and determine whether wildlife can persist in shared landscapes (Kiss, 1990) and in protected areas adjacent to human settlements (Emerton and Mfunda, 1999; Mwakatobe et al., 2014). Fortress conservation, whereby local communities are expelled and excluded from a protected area's resources, has been suggested to be ineffective at reducing human-carnivore conflict (see glossary in **Table 1**) due to its adversarial nature and displacement of stakeholders (Hulme and Murphree, 1999; Galvin and Haller, 2008). In multi-use landscapes, where human communities reside alongside wildlife, neglecting the need for community support can exacerbate conflict, whereas implementing management strategies that communities accept can ameliorate conflict, enhance tolerance, and benefit wildlife (Catalano et al., 2019). Accordingly, it is important for authorities to seek community acceptance to ensure the sustainability and effectiveness of management strategies (**Table 1**).

Areas with large carnivores and pastoralists are of particular interest in human-wildlife conflict studies due to the potential for livestock depredation (Bagchi and Mishra, 2006) and attacks on humans (Shepherd et al., 2014). Despite these challenges, large carnivores are among the most culturally important and emotionally evocative animals to people who live alongside them (Bruskotter et al., 2017; Albert et al., 2018). Previous studies separately examined the effect of the emotions a species elicits, its importance to the local community's culture (hereafter "cultural importance") (**Table 1**), and the amount of livestock depredation it causes on the acceptance of management strategies to reduce conflict between humans and large carnivores. Negative emotions toward wildlife have been suggested to predict acceptance of management strategies that can kill or hurt them, whereas positive emotions have been suggested to predict acceptance of protective management strategies (Jacobs et al., 2014; Sponarski et al., 2015). In addition, the cultural importance placed on wildlife has been suggested to have a positive relationship with conservation-oriented management strategies (Frank, 2016). Other studies found that livestock depredation by large carnivores can predict whether people accept relocation and lethal control (Kaczensky, 1999; Gusset et al., 2009; **Table 1**). Many studies focused on one of the three factors and may have linked them to the acceptance of different management strategies, but did not compare them directly. It therefore remains unclear whether one factor is more influential than the other and should be prioritized for conflict mitigation.

We simultaneously assessed emotions, cultural importance, and livestock depredation to determine which has the greater predictive potential among the Maasai community in the Ngorongoro Conservation Area (NCA), Tanzania. We assessed whether the predictors differ for three large carnivore species—spotted hyenas (hereafter "hyenas"), lions, and leopards—to find the mechanism underlying the acceptance of three management strategies. These species were chosen because they are the primary livestock predators in Tanzania (Kissui, 2008; Mkonyi et al., 2017) and can pose a direct threat to human lives (Peterhans

TABLE 1 | Glossary of main concepts as applied in this study.

Concept	Definition	References
Acceptance	The degree to which someone agrees with, supports, or tolerates a situation or concept on a discrete scale or continuum. When applied to our seven-point scale, it describes cases where a respondent gave a score of > 4.	Treves and Naughton-Treves, 2005
Coexistence	A state in which humans and large carnivores occur in shared landscapes where human interactions with carnivores are governed by institutions that ensure long-term carnivore persistence, social legitimacy, and tolerable levels of risk.	Carter and Linnell, 2016
Cultural importance	The significance that a human community or ethnic group places on or associates with a wild animal; the degree to which the animal plays a role in the social practices, traditions, and/or rituals therein.	Schwartz, 2006
Disgust	An emotion in which a person feels intensely repulsed by the exposure to or the thoughts of a stimulus and wants it to be kept far away.	Rozin et al., 1999
Emotion	Transient, discrete neurological state in an individual brought on by external or internal stimuli. Associated with behavioral responses, physiological conditions, and indicative of a degree of pleasure or displeasure.	Ekman, 1999
Fear	An emotion in which a person feels threatened or intimidated by a stimulus out of a sense of danger.	Lang, 1985
Human-carnivore conflict	Interactions between humans and large carnivores that are deemed problematic, e.g., livestock depredation or man-eating.	Broekhuis et al., 2017
Joy	An emotion in which a person feels happy and positive due to a stimulus.	Watkins et al., 2018
Lethal control	The killing of a wild animal in an effort to reduce the number of wild animals and mitigate human-wildlife conflict, and/or protect domestic animals to improve human livelihoods.	Treves and Naughton-Treves, 2005
Management strategy	A policy implemented by a local governing body or authority to mitigate conflict between humans and carnivores.	Treves and Karanth, 2003
No action	Letting wild animals exist in their natural state without persecution, i.e., maintaining the conservation status quo.	Harcourt et al., 1986
Relocation	Moving a wild animal deemed as a nuisance to human livelihoods to another location in order to mitigate human-wildlife conflict.	McCoy and Berry, 2008
Tolerance	Human willingness to share landscapes with large carnivores.	Lischka et al., 2019

and Gnoske, 2001). Several studies have also suggested that, in other communities, there are differences in the emotions that people have toward the species (Sibanda et al., 2020), the cultural importance the species have (Gebresenbet et al., 2018), the extent of livestock depredation the species cause (Okello et al., 2014; Lichtenfeld et al., 2015), and how people want them managed (Mitchell et al., 2019). Each variable involves different psychological levels and pathways: emotions are linked to affective pathways (inferring feelings or emotions), cultural importance to cognitive pathways (inferring thoughts or beliefs; Healey and Grossman, 2018), and livestock depredation is largely external to individual control. By simultaneously investigating the predictive potential of these variables on the three carnivores, we can disentangle their respective effects, assess whether the differences hold true among the NCA Maasai, and understand the mechanisms that shape acceptance across the large carnivore guild. We studied the acceptance of no action, relocation, and lethal control, three management strategies commonly applied where large carnivores and humans co-occur (Linnell et al., 1997; Treves and Karanth, 2003; Karanth and Gopal, 2005; **Table 1**). All three management strategies have a precedent for being applied in the NCA and are within the mandate of the Ngorongoro Conservation Area Authority, the local governing body (Ikanda and Packer, 2008). Other management strategies for large carnivores (e.g., compensation, improved construction of livestock corrals, or accompanying livestock on foot) have also been applied in the NCA, but we opted to select these three as they are the most commonly used in our study area and are more widely applicable to other study areas, irrespective of their expected effectiveness (Van Eeden et al., 2018).

Previous studies have suggested that animals can trigger emotions in people that can predict the acceptance of management strategies (Gore et al., 2009; Jacobs, 2009). For example, the positive emotion joy (**Table 1**) predicted the acceptance of the protection of chipmunks in Italy (Cerri et al., 2020). Negative emotions can also predict management strategy acceptance. Disgust and fear (**Table 1**) toward carnivores have been suggested to undermine conservation efforts and be more significant drivers of human-carnivore conflict than livestock depredation (Dickman, 2010). In communities bordering Iguaçu National Park, Brazil, fear of pumas (*Puma concolor*) was found to be lower than fear of jaguars (*Panthera onca*); the presence of jaguars was rejected while the presence of pumas was accepted (Conforti and de Azevedo, 2003). Lions were found to bring negative emotions among farmers in Zimbabwe which in turn predicted how accepting they were of protective management strategies toward lions (Sibanda et al., 2020). Hyenas tend to bring about negative emotions across human communities, which in turn may drive a desire to see them killed (Glickman, 1995). We predicted that joy would be a negative predictor of relocation and lethal control, and a positive predictor of the acceptance of no action. In contrast, we predicted that disgust and fear would be positive predictors of relocation and lethal control and negative predictors of no action.

The cultural importance of a wildlife species can have ramifications on how likely people are to accept different management strategies (Dickman, 2010). The more culturally important or iconic a species is, the more likely a community is to accept protective management strategies for the species and the less likely they are to accept lethal control or other invasive management strategies. The high cultural importance of the lion has been suggested to have led to a general acceptance of lion conservation among the Maasai (Hazzah et al., 2019). High cultural importance placed on blackbuck antelope (*Antilope cervicapra*) among the Bishnoi in India was also found to predict their acceptance of conservation of that species (Hall and Chhangani, 2015). In Australia, cultural importance was found to be a negative predictor for the acceptance of lethal control of koalas (*Phascolarctos cinereus*) (Drijfhout et al., 2020). Communities also may place different cultural importance on different species of large carnivore. For example, a study in Kenya found that leopards were more culturally important to the Samburu community than African wild dogs, which in turn predicted the differing acceptance of the protection of the two species (Mitchell et al., 2019). Thus, to understand the relationship between cultural importance and the acceptance of different management strategies for wildlife, it is important to recognize inter-specific differences in perception. We predicted that cultural importance would be a positive predictor of acceptance of no action and a negative predictor of acceptance of relocation and lethal control.

The focus of human-carnivore conflict studies has traditionally been livestock depredation, which has also been suggested to predict the acceptance of management strategies. Depredation was found to have a positive correlation with lethal control of carnivores in South Africa (Daly et al., 2006). After disease, hyenas were found to be the second-most important source of livestock loss, and communities which suffered more livestock depredation by carnivores were more likely to accept lethal control in Tanzania (Nyahongo, 2007). Livestock depredation was also a positive predictor of acceptance of lethal control of Brazilian carnivores (Engel et al., 2016). We predicted that reported livestock depredation, i.e., perceived conflict, would be a significant negative predictor of the acceptance of no action and a significant positive predictor of the acceptance of relocation and lethal control.

MATERIALS AND METHODS

Study Area

This study took place in the NCA located in Tanzania (03°12′36′′S 35°27′36′′E; **Figure 1**). The NCA is a multi-use protected area and United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site noted for its high density of large mammals and popularity as a tourist destination (Charnley, 2005). It is inhabited by members of the Maasai tribe, a semi-nomadic pastoralist ethnic group that ranges from central Kenya to southern Tanzania (Fratkin, 2001). The NCA has a double mandate to conserve wildlife while protecting the interests of the Maasai (Charnley, 2005). Within the NCA is the Ngorongoro Crater, a 300 km^2 volcanic caldera with high densities of both hyenas and lions on the Crater floor and leopards along the rim forests (Packer et al., 1991;

Höner et al., 2012). The wider NCA also supports populations of hyenas, lions, and leopards. The Maasai and cattle populations in the NCA have grown from ~8,000 and 162,000 upon the establishment of the NCA in 1959 to ~93,000 and 243,000, respectively, as of 2017, putting them at increased risk of conflict with carnivores (National Bureau of Statistics Tanzania, 2017).

Survey

Our survey instrument included five sections with closed questions. Section 1 focused on livestock depredation. Respondents were asked to report the average number of cattle, sheep, goats, and donkeys that they lost annually over the past 3 years due to depredation by hyenas, lions, and leopards and to drought/disease. Section 2 focused on a set of Wildlife Value Orientations (Manfredo et al., 2009). Sections 3–5 were used to score the cultural importance of, emotions (joy, disgust, and fear) toward, and the acceptance of three management strategies (no action, relocation, and lethal control) for each carnivore. Sections 2–5 relied on the usage of a discrete, numeric scale, where respondents would respond to a prompt and give a score between 1 (strongly disagree/reject) and 7 (strongly agree/accept). Section 6 focused on socio-demographic factors. Due to the Cronbach's Alpha (internal consistency) scores for the domination ($\alpha = 0.15$) and mutualism ($\alpha = 0.67$) dimensions of Wildlife Value Orientations falling below the critical threshold of 0.70, they were not included in our study. Furthermore, other prompts in the questionnaire were not included in the analyses for this study; they were not the focus of this comparative study on the predictive potential of different and often separately tested variables.

We first tested the survey instrument and explored the suitability of using selected items with the Maasai in a pilot survey conducted in February 2018 with 20 participants in Ngorongoro ward (**Supplementary Material**, Appendix A). The main survey (**Supplementary Material**, Appendix B) was then undertaken in March 2019 with 100 respondents. Respondents who participated in the pilot survey were not interviewed again for the main survey. The beginning and end time, ward, and geographic coordinates were noted for each questionnaire while further information such as the respondents' names were not included to maintain anonymity.

To accurately represent the local community, the 100 questionnaires were split between 50 men and 50 women and categorized into the following age sets: *endasati* ($n = 25$) and *siangiki* (25) for elder and young women, respectively, and *ilmoruak* ($n = 17$), *korianga* ($n = 17$), and *morani* ($n = 16$) for elder, middle-aged, and young men, respectively (McCabe et al., 2014; National Bureau of Statistics Tanzania, 2017). On each survey day, we visited pre-selected wards (**Figure 1**) and walked through the villages until an individual suspected to be of a target demographic was randomly sighted and approached between 08:00 h and 18:00 h. The aim of the survey was introduced and respondents were asked if they consented to participation and to state their age class and gender. Each respondent represented a single household. Owing to low literacy amongst the Maasai in the NCA (Goldman and Milliary, 2014), questionnaire items were read aloud, translated into Maa—their native language—and responses again translated from Maa to English, then recorded on a printed questionnaire copy. Participation by respondents was voluntary and unpaid. Each respondent was then presented with photographs of the three carnivores in this study as well as the African wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), and striped hyena (*Hyaena hyaena*), three carnivores that are transient in the parts of the NCA we covered (Kennedy and Kennedy, 2014). Respondents were asked to name the carnivores; all 100 respondents accurately identified the carnivores.

Quantification of Livestock Depredation

We quantified herd size and livestock loss based on the number of heads of each species of livestock owned by each respondent and on the number of heads that died. Total financial loss incurred by each respondent was calculated by multiplying the number of heads of the livestock species lost by their per capita financial value on the local market. At the time of the study, NCA market prices for cattle, sheep, goats, and donkeys were TSH 400 000 (USD 174), TSH 110 000 (USD 48), TSH 110 000 (USD 48), and TSH 200 000 (USD 87), respectively. Proportional financial loss was then calculated by dividing the total financial value lost to the particular carnivore divided by the financial value of the livestock owned by the respondent prior to the loss. We used proportional financial loss (hereafter "livestock depredation") instead of the raw number of livestock heads that died as a predictor because (i) the market value differs between livestock species and may impact the perception of livestock depredation by respondents, (ii) herd size varies greatly in the NCA (this study; National Bureau of Statistics Tanzania, 2017), and (iii) the relative cost of livestock depredation may matter more than the absolute cost in shaping the perception of an experience as negative (Mkonyi et al., 2017). For an overview of the number of heads of the different livestock species that were killed by the different carnivores and the ensuing financial costs, see **Supplementary Table 1**.

Data Analyses

Statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020). The threshold for statistical significance was set to $\alpha = 0.05$, and data are presented as mean ± S.E. unless stated otherwise.

We compared the scores for the emotions of joy, disgust, and fear each carnivore elicited and their cultural importance using Friedman rank sum tests and Dunn *post-hoc* pairwise multiple comparisons with Bonferroni corrected p-values (package "dunn.test"; Dinno, 2017). Responses to the prompts on emotions, cultural importance, and the acceptance of management strategies were plotted as diverging stacked bar plots (package "likert"; Bryer and Speerschneider, 2016).

The livestock depredation caused by each carnivore (independent variable with three levels: hyena, lion, and leopard) was compared using a generalized linear mixed effects model (GLMM), with a beta distribution and logit link (package "glmmTMB"; Brooks et al., 2017; Douma and Weedon, 2019). Proportions (for the response variable, livestock depredation)

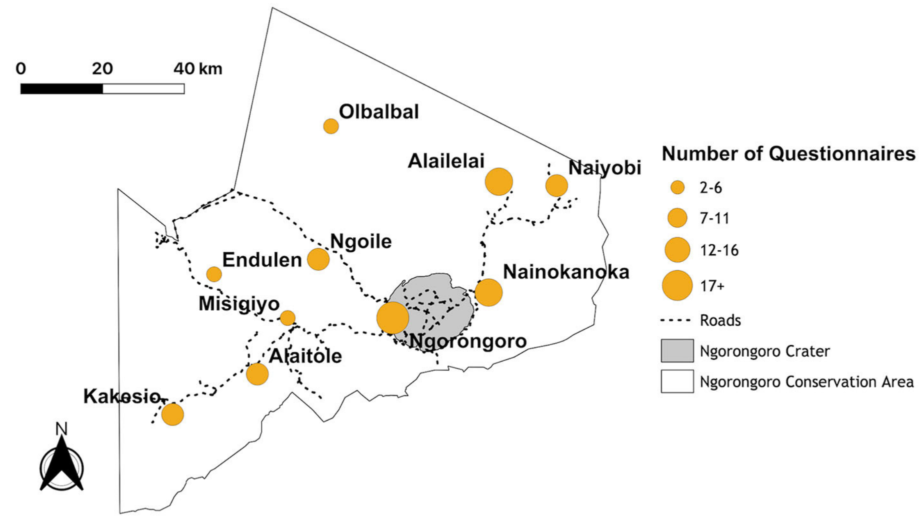

FIGURE 1 | Location and distribution of the 100 questionnaires conducted in the Maasai community living in Ngorongoro Conservation Area, Tanzania. The size of the orange circles indicates the number of questionnaires conducted within each of the ten labeled wards.

were transformed using the formula for beta distributions with values that include 0 and/or 1: $y^*(n-1)+0.5)/n$, where y is the original proportion and n is the sample size (100 respondents * 3 carnivores = 300) (Cribari-Neto and Zeileis, 2009). Because each respondent was assigned a value for livestock depredation pertaining to each carnivore, data included repeated measures. We therefore included the unique identifier for each respondent as a random factor.

The influence of the type of management strategy (no action, relocation, lethal control), the carnivore species (hyena, lion, leopard), emotions (joy, disgust, fear), cultural importance, and livestock depredation on the acceptance scores was tested using an ordinal logistic regression (OLR) model (function "clmm" in package "ordinal"; Christensen, 2019). We included an interaction term between management strategy and all other covariates to disentangle and quantify the effects of the predictors. The identity of the respondent (100 levels) was included as a random factor.

To avoid multicollinearity, numeric predictors were centered at their means using function "center.numeric" from the package "psycholing" (Fraundorf, 2020). All predictors fell below the critical variance inflation factor (VIF) threshold of 10 (package "HH"; James et al., 2013; Heiberger, 2020). Note that most studies involving a Likert-type dependent variable, i.e., a score on a discrete ordinal scale, traditionally conduct ordinary least-squares regressions (OLS) (Bishop and Herron, 2015; Bürkner and Vuorre, 2019). When applied to ordinal scores, metric models such as OLS assume that spacing between each score is the same, e.g., that a switch from 1 to 2 involves the same cognitive process as a switch from score 4–5 on a seven-point scale. This assumption is likely to be violated (Liddell and Kruschke, 2018). OLR, which allows for cognitive flexibility and account for the ordered nature of Likert-type data, are therefore more appropriate (Harrell, 2015).

The significance of the effects of each focal predictor and the interaction terms on acceptance was assessed using likelihood ratio tests (function "anova" in package "stats;" R Core Team, 2020). The likelihood ratio tests determined the marginal contribution of the focal predictor to the full model by comparing the fit of the full model with that of a reduced model with the focal predictor removed.

Both the GLMM and OLR models generated estimates as log(odds) which we converted to odds ratios and 95% confidence intervals using the function "exp(confint(model))" for ease of interpretation. Odds ratios > 1 and odds ratios < 1 indicate a relative increase and decrease, respectively, in the likelihood of the dependent variable to increase by one unit when the predictor variable increases by one unit. For example, if the odds ratio for a given predictor in the OLR is 1.50, then a one-unit increase in the predictor (e.g., from 4 to 5) leads to the probability of an increase (e.g., from score 4 to score 5) in acceptance being 50% higher when all other variables in the OLR are held constant. In the case of the livestock depredation GLMM, a one-unit "increase" in the predictor refers to a switching of the carnivore species—the reference species was set as the hyena, so a one-unit "increase" in this model refers to a shift in the predictor from hyena to lion or leopard. The OR expressed therefore refers to the odds of livestock depredation increasing when hyenas are replaced by lions or leopards. An OR > 1 would therefore mean that the focal species causes more livestock depredation than hyenas, and the opposite would be true for an OR < 1. Further information on how to construct and interpret OLR using the "clmm" function can be found in Lorenzo-Arribas (2019, p. 57–71). Cumulative predicted probabilities of acceptance (score > 4) of the management strategies as a function of the different predictors were calculated based on the OLR with the package "emmeans" (Lenth, 2021) and then plotted using the package "ggplot2" (Wickham, 2016).

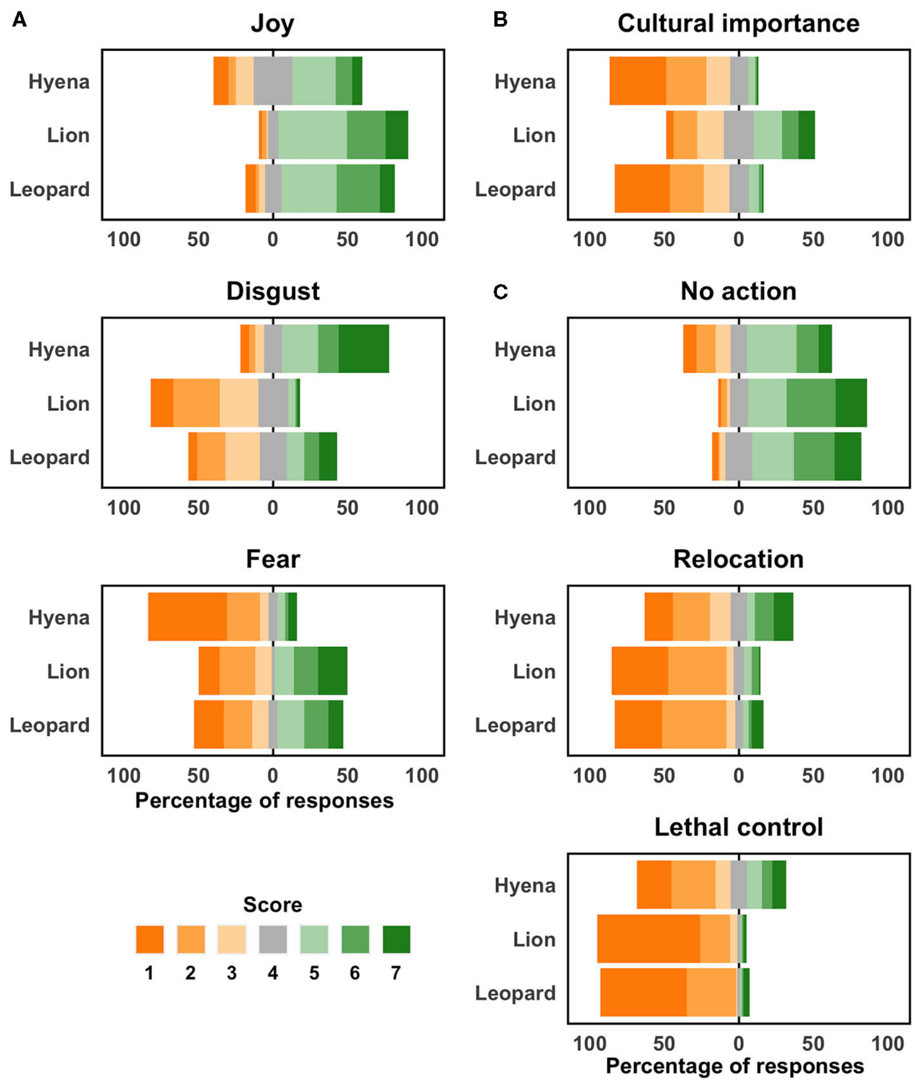

FIGURE 2 | Distribution of scores (percentage of responses) for the emotions joy, disgust, and fear **(A)**, cultural importance **(B)**, and the acceptance of the management strategies no action, relocation, and lethal control **(C)** toward hyenas, lions, and leopards by Maasai pastoralists in Ngorongoro Conservation Area, Tanzania. Data correspond to scores on a seven-point scale in questionnaires ($n = 100$). Diverging stacked bar plots display the distribution of scores ranging from 1 (strongly disagree/reject) to 7 (strongly agree/accept), with 4 representing a neutral score. The left side (orange range) of the figure shows the percentage in disagreement and the right side (green range) the percentage in agreement with the prompt.

RESULTS

Emotions

47% of respondents felt joy toward hyenas (score > 4), compared to 87% for lions and 76% for leopards (**Figure 2A**). 72% of respondents found hyenas disgusting (score > 4), compared to 8% for lions and 34% for leopards. 13% of respondents feared hyenas (score > 4), in contrast to 49% for lions and 44% for leopards. Scores for the emotions differed significantly between carnivores (Friedman test; joy: $\chi^2 = 41.58$, $df = 2$, $p < 0.001$; disgust: $\chi^2 = 88.10$, $df = 2$, $p < 0.001$; fear: $\chi^2 = 70.54$, $df = 2$, $p < 0.001$). Hyenas brought less joy ($\text{median}_{\text{hyena}} = 4.0$) than both lions ($\text{median}_{\text{lion}} = 5.0$, $p < 0.001$) and leopards ($\text{median}_{\text{leopard}} = 5.0$, $p < 0.001$). There was no difference in joy toward lions and leopards ($p = 0.26$). Respondents felt greater disgust toward hyenas ($\text{median}_{\text{hyena}} = 5.0$) than to both lions ($\text{median}_{\text{lion}} = 3.0$; $p < 0.001$) and leopards ($\text{median}_{\text{leopard}} = 4.0$; $p < 0.001$), and greater disgust toward leopards than lions ($p < 0.001$). Hyenas were feared less ($\text{median}_{\text{hyena}} = 1.0$) than both lions ($\text{median}_{\text{lion}} = 4.0$, $p < 0.001$) and leopards ($\text{median}_{\text{leopard}} = 3.5$, $p < 0.001$), whereas fear of lions and leopards did not significantly differ ($p = 0.39$).

Cultural Importance

7% of respondents found hyenas culturally important (score > 4), compared to 41% for lions and 10% for leopards (**Figure 2B**). Respondents attributed different cultural importance to the carnivores ($\chi^2 = 90.08$, $df = 2$, $p < 0.001$). Hyenas were seen as culturally unimportant overall ($median_{hyena} = 2.0$) and less culturally important than lions, which were seen as neither culturally important or unimportant ($median_{lion} = 4.0$; $p < 0.001$). There was no difference in cultural importance between hyenas and leopards ($median_{leopard} = 2.0$; $p = 0.85$). Leopards were seen as less culturally important than lions ($p < 0.001$).

Livestock Composition and Depredation

All respondents belonged to a household that owned livestock, with a mean of 137.4 ± 26.8 heads of livestock per household. Nearly all respondents (97%) owned herds that were composed of at least two species. Respondents owned a mean of 40.2 ± 5.4 cattle, 70.9 ± 20.4 sheep, 23.0 ± 3.6 goats, and 3.3 ± 0.5 donkeys. The carnivores differed in the livestock depredation they caused. Compared to hyenas (beta GLMM; OR = 0.14, $CI_{95\%}$ = 0.11–0.16, $p < 0.001$), both lions (OR = 0.25, $CI_{95\%}$ = 0.19–0.33, $p < 0.001$) and leopards (OR = 0.35, $CI_{95\%}$ = 0.27–0.45, $p < 0.001$) caused less livestock depredation. Lions also caused less livestock depredation than leopards (OR = 0.72, $CI_{95\%}$ = 0.55–0.94, $p = 0.016$). Hyenas accounted for a mean of 13.4 ± 1.3% of livestock depredation, lions 1.9 ± 0.3%, and leopards 4.1 ± 0.7% (**Supplementary Figure 1**).

Acceptance of Management Strategies

The majority of respondents accepted (score >4) no action for all three carnivores (hyenas: 57%, lions: 80%, leopards: 73%; **Figure 2C**). In contrast, both relocation and lethal control were mostly rejected (relocation: hyenas: 31%, lions: 11%, leopards: 14%; lethal control: 26%, 4%, and 6%).

Management strategy (OLR, likelihood ratio test; LR = 563.22, $p < 0.001$) and carnivore species (LR = 36.82, $p < 0.001$) had significant effects on acceptance scores (**Figure 3**; **Table 2**). Acceptance of no action was similar for all three carnivore species. In contrast, acceptance scores of relocation and lethal control were higher for hyenas than for lions and leopards (**Supplementary Tables 2**, **3**). There was no difference in acceptance scores of relocation and lethal control between lions and leopards (**Supplementary Table 4**).

Emotions had a significant effect on the acceptance score of management strategies (LR = 97.80, $p < 0.001$). Joy had a strong effect (LR = 68.31, $p < 0.001$), disgust a weak effect (LR = 7.20, $p = 0.066$) and fear no effect (LR = 3.94, $p = 0.27$) (**Table 2**; **Figure 4A**). The effect of joy differed between the management strategies (**Table 2**). It had a strong, positive effect on the acceptance of no action and a negative effect on the acceptance of relocation and lethal control. When the joy score changed from 1 to 7, predicted acceptance changed from 27% ($CI_{95\%}$: 14–40%) to 83% ($CI_{95\%}$: 77–89%) for no action, from 26% ($CI_{95\%}$: 14–39%) to 14% ($CI_{95\%}$: 8–19%) for relocation and 37% ($CI_{95\%}$: 21–53%) to 2% ($CI_{95\%}$: 1–4%) for lethal control (**Figure 4A**). The effect of disgust also differed between the management strategies (**Table 2**). It had no significant effect on the acceptance of no action and relocation but a weak, positive effect on the acceptance of lethal control. When the disgust score changed from 1 to 7, predicted acceptance changed from 71% ($CI_{95\%}$: 61–80%) to 60% ($CI_{95\%}$: 49–71%) for no action, from 15% ($CI_{95\%}$: 8–21%) to 21%

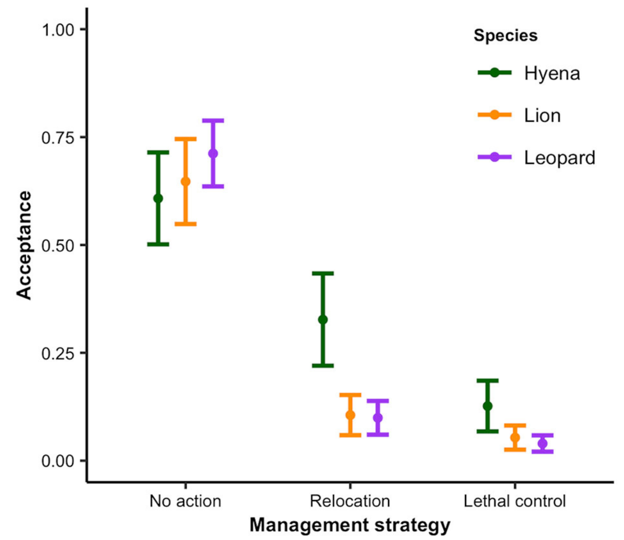

FIGURE 3 | Cumulative predicted probability of the acceptance (score > 4) of no action, relocation, and lethal control as management strategies toward hyenas, lions, and leopards by Maasai pastoralists in Ngorongoro Conservation Area, Tanzania. Points represent mean predicted probabilities from an ordinal logistic regression model and bars represent the 95% confidence intervals when continuous predictors are held at their population means.

($CI_{95\%}$: 14–29%) for relocation and 5% ($CI_{95\%}$: 2–7%) to 12% ($CI_{95\%}$: 6–17%) for lethal control (**Figure 4A**).

Cultural importance had a significant effect on the acceptance of management strategies (LR = 20.39, $p < 0.001$; **Table 2**). It was positive for no action and weakly negative for relocation and lethal control. When the score for cultural importance changed from 1 to 7, predicted acceptance changed from 58% ($CI_{95\%}$: 50–66%) to 79% (69–89%) for no action, from 23% ($CI_{95\%}$: 17–29%) to 9% ($CI_{95\%}$: 4–15%) for relocation, and from 11% ($CI_{95\%}$: 7–15%) to 3% ($CI_{95\%}$: 1–5%) for lethal control (**Figure 4B**).

Livestock depredation had a significant effect on the acceptance of management strategies (LR = 14.17, $p = 0.003$; **Table 2**). It had no effect on no action and lethal control but a negative effect on relocation. When proportional financial loss (livestock depredation) changed from 0.0 to 0.8, predicted acceptance changed from 65% ($CI_{95\%}$: 59–71%) to 73% ($CI_{95\%}$: 40–100%) for no action, from 22% ($CI_{95\%}$: 17–27%) to 1% ($CI_{95\%}$: 0–2%) for relocation and 8% ($CI_{95\%}$: 5–11%) to 0% ($CI_{95\%}$: 0–1%) for lethal control (**Figure 4C**).

DISCUSSION

Our results suggest that the Maasai pastoralists living in the NCA are generally against the relocation and lethal control of large carnivores. Our results further suggest that the acceptance of management strategies is strongly influenced by emotions and cultural importance and that emotions and cultural importance are stronger predictors of the acceptance of management strategies than livestock depredation. These

TABLE 2 | Variation in acceptance scores by Maasai pastoralists as a function of management strategies, carnivore species, emotions, cultural importance, and livestock depredation.

Predictor	OR	$CI_{95\%}$	*p*
Threshold coefficients			
1|2	0.04	0.03–0.07	-
2|3	0.21	0.13–0.33	-
3|4	0.34	0.21–0.53	-
4|5	0.65	0.41–1.01	-
5|6	1.71	1.10–2.68	-
6|7	5.62	3.48–9.06	-
Management strategies			
Relocation	**0.31**	**0.17–0.59**	**<0.001**
Lethal control	**0.09**	**0.05–0.18**	**<0.001**
Species			
Lion	1.18	0.60–2.37	0.64
Leopard	1.59	0.89–2.85	0.12
Emotions			
Joy	**1.55**	**1.31–1.82**	**<0.001**
Disgust	0.92	0.81–1.06	0.24
Fear	1.03	0.93–1.14	0.59
Cultural importance	**1.19**	**1.04–1.36**	**0.013**
Livestock depredation	1.57	0.17–14.97	0.70
Interaction terms			
Relocation*Lion	**0.21**	**0.07–0.57**	**0.002**
Lethal control*Lion	**0.33**	**0.11–0.96**	**0.042**
Relocation*Leopard	**0.14**	**0.06–0.34**	**<0.001**
Lethal control*Leopard	**0.18**	**0.07–0.44**	**<0.001**
Relocation*Joy	**0.56**	**0.44–0.71**	**<0.001**
Lethal control*Joy	**0.37**	**0.29–0.48**	**<0.001**
Relocation*Disgust	1.18	0.97–1.44	0.10
Lethal control*Disgust	**1.28**	**1.05–1.57**	**0.017**
Relocation*Fear	1.05	0.91–1.21	0.53
Lethal control*Fear	0.90	0.76–1.05	0.17
Relocation*Cultural importance	**0.70**	**0.57–0.85**	**<0.001**
Lethal control*Cultural importance	**0.67**	**0.54–0.83**	**<0.001**
Relocation*Livestock depredation	**0.01**	**0.00–0.19**	**0.003**
Lethal control*Livestock depredation	0.22	0.01–6.59	0.39

Shown are the odds ratios (OR), their associated 95% confidence intervals ($CI_{95\%}$), and p-values for each predictor, as derived from an ordinal logistic regression model (individual-level random effect variance = 0.07). OR > 1 and OR < 1 indicate a relative increase and decrease, respectively, in the acceptance score associated with a 1-unit increase or shift in the focal predictor when all other covariates are held constant at their population mean or reference level. The reference carnivore species is the hyena and the reference management strategy is no action. Threshold coefficients refer to the cumulative probability that an acceptance score is at or below the threshold cut point, e.g., the OR for the threshold 2|3 compares the probability of the acceptance score falling within the range of 1–2 to the probability of the acceptance score falling within the range of 3–7. Data in bold were deemed significant ($p < 0.05$).

variables had the most significant results and had large effect sizes. The effect of emotions was mostly driven by joy: a positive effect on no action and a negative effect on relocation and lethal control, as predicted. The effects of the positive emotion joy are consistent with previous findings that suggested that joy is connected to a desire not to see animals killed or moved (Sponarski et al., 2015). Disgust had only a weak effect and fear had no significant effect on the acceptance of management strategies. The effect of cultural importance was positive for no action and negative for relocation and lethal control, as predicted. Despite controlling for several important predictors in our model, there was a significant difference in the acceptance of relocation and lethal control between the carnivores. These differences warrant further investigation to identify additional drivers of the inter-specific variation in acceptance of invasive management strategies within the large carnivore guild.

The key role of emotions and cultural importance as predictors of the acceptance of management strategies has potential conservation implications and applications. Being cognitive and affective variables, they are influenced by shifts in external factors. For emotions, our findings may facilitate

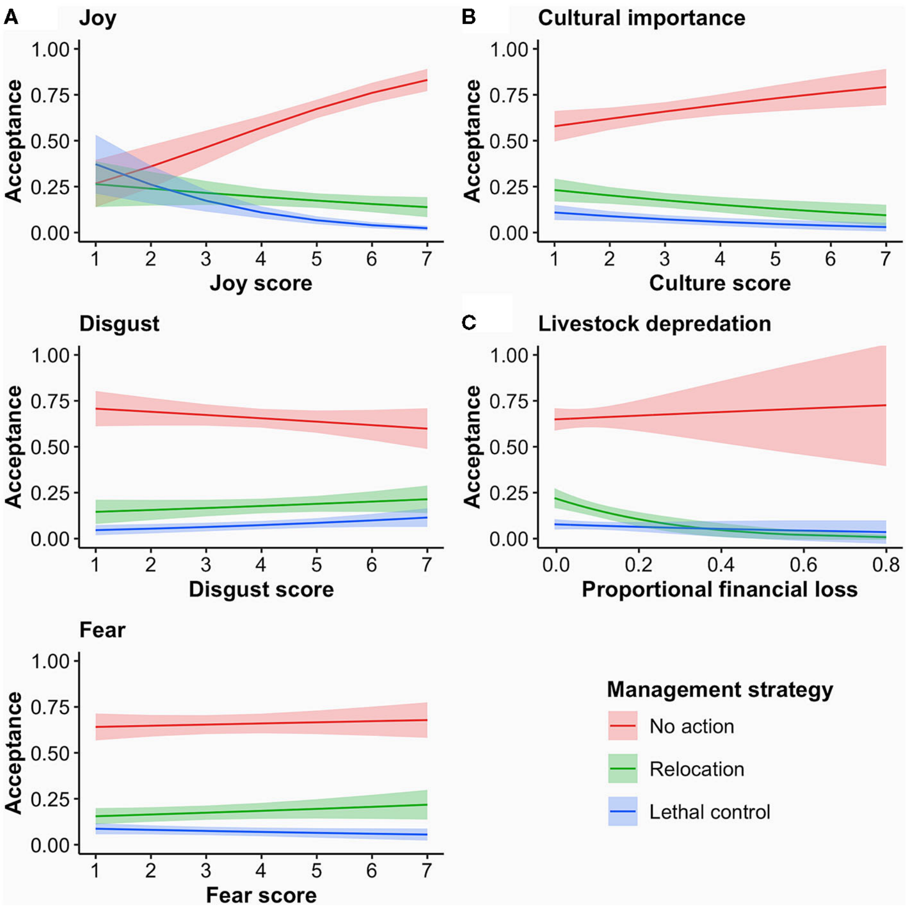

FIGURE 4 | Cumulative predicted probability of the acceptance (score > 4) of no action, relocation, and lethal control as management strategies toward hyenas, lions, and leopards by Maasai pastoralists in Ngorongoro Conservation Area, Tanzania. Plots show how emotions **(A)**, cultural importance **(B)**, and livestock depredation **(C)** influenced the acceptance of the management strategies. For emotions and cultural importance, scores range from 1 (strongly disagree/reject) to 7 (strongly agree/accept), with 4 representing a neutral score. For livestock depredation, the x-axis is limited to the range of observed values (0.0–0.8). Lines represent mean predicted probabilities from an ordinal logistic regression model and shading represents the 95% confidence intervals when continuous predictors are held at their population means and using the mean effect of the carnivore species.

local authorities' investment in outreach initiatives. We found that the positive emotion joy was a more important predictor of management strategy acceptance than the more negative emotions disgust and fear; we recommend an increased emphasis on positive emotions rather than the traditional focus on negative emotions toward wildlife (Espinosa and Jacobson, 2012). Education and awareness about predators can sometimes ameliorate negative emotions (Bruskotter and Wilson, 2014; Lyngdoh et al., 2017) and mitigate conflict due to improved knowledge of the risks and drivers of conflict (Treves and Karanth, 2003). As charismatic species such as lions continue to be represented positively, emotions toward these animals remain positive while negatively represented species continue to be subject to negative emotions (Albert et al., 2018). To incite change, it may be fruitful to depict hyenas positively in the NCA. For example, mentioning the value of social support in hyena society (Vullioud et al., 2019) may place them in a positive light due to the Maasai community's strong family focus (Kipuri, 2020) and further reduce the acceptance of relocation or lethal control of hyenas. Moreover, ecosystem services that hyenas provide as predators and scavengers may contribute to the control of diseases (O'Bryan et al., 2018) by reducing disease transmission within livestock herds and between wild herbivores and livestock (Stronen et al., 2007). This could also be highlighted as a benefit of having hyenas around. Such efforts can be put into place at workshops and outreach efforts for schoolchildren in order to instill positive emotions toward carnivores in Maasai community members from a young age (Mkonyi et al., 2017). There is a precedent for the efficacy of such efforts elsewhere, with children (Johansson et al., 2016) and adults alike (Breuer et al., 2020). The efficacy of such efforts can be enhanced by involving societal "influencers," e.g., elders with considerable reach and power (Veríssimo et al., 2019). Regardless, such efforts should only be done with collaborative, enthusiastic involvement from the community side and in a way that benefits local stakeholders (Berkes, 2004).

Regarding cultural importance, intergenerational change and concurrent sedentarism has been suggested to result in increased acceptance for wildlife conservation (Laverty et al., 2019). However, it may also lead to reduced physical, spiritual, or emotional contact with wildlife, e.g., by losing touch with traditional values and practices that bring humans and wildlife closer together. For example, lion killing by *moranis*, in a symbolic coming-of-age ceremony, has become rarer (Western et al., 2019) and may have reduced the importance of lions over time. This may explain the "neutral" median score lions received for cultural importance. In the NCA, the Maasai are required to live a traditional semi-nomadic lifestyle to protect wildlife habitats (Lawuo et al., 2014), which may limit shifts in the cultural importance of different carnivores. Capitalizing on the knowledge of the cultural importance of different carnivores and its predictive potential would enable authorities to influence the acceptance of different management strategies by easing or tightening current rules about lifestyles that are in place. It would therefore be prudent to collect long-term data on local scores for the cultural importance of wildlife to detect shifts over time, compare cultural importance scores between older and younger generations, and assess how scores change with different policies. It may also help to identify where and to what extent different management strategies will be accepted and be effective at limiting conflict, e.g., as with the Lion Guardians model in Kenya (Hazzah et al., 2019).

In contrast to our predictions, livestock depredation was only a significant predictor for the acceptance of relocation, and the relationship was negative. While this result may seem surprising, given that many Maasai are wholly dependent on their livestock (McCabe et al., 2014), several explanations may be valid. Firstly, with increasing livestock depredation, the predicted acceptance of relocation decreased to a point where it was strongly rejected. This may indicate that following higher rates of livestock depredation, the Maasai become wary of management strategies such as relocation which risk having the carnivores return again (McCoy and Berry, 2008). Secondly, disease and drought were much greater sources of livestock loss than livestock depredation by all three carnivores combined, which may buffer the effect of livestock depredation. It also may be partly due to the fact that the tourism industry is a source of employment for the Maasai community and may further mask the effects of livestock depredation (Homewood and Rodgers, 2004; Melita, 2014). It is also plausible that the Maasai in the NCA are accustomed to livestock depredation as an aspect of day-to-day life, as it has been unavoidable for generations. For instance, there may be an interplay between historical livestock depredation by hyenas and the negative emotions associated with them; once these long-term trends become entrenched in local perceptions, they may mask the effect of recent livestock depredation itself and instead be picked up by emotions. A similar result was found in Bangladesh, where livestock owners that were subject to the greatest perceived conflict with tigers (*Panthera tigris*) were the most tolerant of tigers; the authors posited that a greater focus on socio-psychological drivers of tolerance would have been useful to disentangle the effects of livestock depredation and other factors (Inskip et al., 2016). This lies in contrast to a study in Namibia which found that farmers tolerated carnivores the most in areas where livestock depredation was the lowest (Lindsey et al., 2013). However, the study did not assess how values or emotions that were already in place may have predicted tolerance or the acceptance of management strategies. We contend it is crucial to simultaneously consider socio-psychological factors such as emotions and cultural importance along with livestock depredation to assess which is more important as predictors of the acceptance of management strategies (Jacobsen et al., 2020). Further examination of the acceptance of other management strategies which we did not include but can also promote coexistence, such as improving livestock corrals or compensation schemes, may improve understanding of the predictive potential of livestock depredation in comparison to other factors.

It is worth recognizing that our approach—to begin by asking about livestock depredation and then going into emotions, cultural importance, and management strategies—may have introduced a bias by having respondents associating the carnivores with livestock loss. Despite this possibility, we argue that any potential effect was not severe, owing to the fact that the respondents displayed a general acceptance of no action toward the carnivores in our study, a rejection of relocation and lethal control, and views that are in accord with other studies on Maasai-carnivore relationships (Kissui, 2008; Goldman, 2011). Furthermore, livestock depredation ended up being a weak predictor, and only for one management strategy, despite being introduced first.

In summary, this study demonstrates the importance of assessing emotions and cultural importance in human-carnivore conflict studies and the importance of accounting for potential variations in acceptance of different management strategies and species. Our findings have affirmed the role of positive emotions in relation to human relationships with wildlife (Buijs and Jacobs, 2021) and confirmed the importance of considering both affective and cognitive factors (Dechner, 2021). They also question the widespread view that livestock depredation is the most important issue to focus on in human-carnivore studies. Further, we have highlighted the importance of considering the different emotions that people have toward species within the same guild—cultural and psychological factors may play a role. Specifically to the Maasai, we have underpinned the importance of different carnivores to their culture and their acceptance of different strategies, forming a basis for coexistence based on various factors. Because the effects of the factors may be direct and indirect (Teixeira et al., 2020), investigating these relationships may disentangle effects and help understand the complex processes associated with tolerance of wildlife and how human cognitions interact with ecological dimensions. In particular, it would be important to understand the interplay between the different factors in order to detect any mediating effects between predictors and their relationship with the acceptance of management strategies. Human-carnivore conflict remains a challenging and complex issue, but understanding the best predictors of the acceptance of management strategies paves the way for authorities to implement locally-accepted initiatives geared toward coexistence between people and wildlife.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are publicly available. This data can be found here: https://doi.org/10.6084/m9.figshare.14780058.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by The Tanzania Wildlife Research Institute, the Tanzania Commission for Science and Technology, and the Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research under approval number 2018-01-03. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

Conceptualization: AD, ED, MJ, TS, and OH. Methodology: AD, ED, MJ, JN, TS, and OH. Formal analysis: AD and TS. Investigation: AD and JN. Resources: JN and OH. Data curation: AD. Writing of original draft: AD, ED, TS, and OH. Review and editing of draft: AD, ED, MJ, TS, and OH. Supervision: TS and OH. Project administration: AD, JN, and OH. Funding acquisition: AD and OH. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2021.691975/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplementary Material

Table of contents

Appendix A: Pilot Questionnaire

1. Experiences

[Start with introduction and small talk – build trust. Then move on to identification test. Then the questions]

Livestock predation:

a) How many cattle, sheep, goats, and donkeys do you lose every year to hyenas?

b) How many cattle, sheep, goats, and donkeys do you lose every year to lions?

c) How many cattle, sheep, goats, and donkeys do you lose every year to leopards?

d) How many cattle, sheep, goats, and donkeys do you lose every year to cheetahs?

e) How many cattle, sheep, goats, and donkeys do you lose every year to wild dogs?

1.1. What other causes of death do you have to your livestock herds (e.g. drought, disease, accidents)? Do you lose more livestock through predators or the other causes?

1.2. How much money do you lose yearly to predation on livestock, on average? (calculate ourselves based on market price)

1.3. Have you directly observed hyenas, or any other predator, attack your livestock (both at the boma and while herding)?

1.4. Can you tell, based on tracks or carcass evidence, which species of predator attacked your livestock?

1.5. Have you or anyone in your family been attacked by a hyena or another predator?

1.6. How do predators kill your livestock (e.g. approaching bomas at night, attacking livestock lost in the forest)?

1.7. Have you attempted to prevent hyenas or other predators from attacking your livestock without killing them? If so, how (e.g. bells, light, banging pots and pans, dogs, throwing stones)? Does this method work?

1.8. What do you do after a hyena attacks your livestock?

1.9. What do the authorities provide as a reward for living with carnivores? Is this sufficient?

1.9.1. If it is not sufficient, what could the authorities provide so that you can live happily together with carnivores?

2. Values

Domination

People can kill wildlife if they think it poses a threat to their life or property.

1 2 3 4 5 6 7

The needs of humans should be over wildlife protection.

1 2 3 4 5 6 7

Killing animals is cruel and inhumane to animals.

1 2 3 4 5 6 7

Killing an animal does not respect the life of the animal.

1 2 3 4 5 6 7

Mutualism

People and wildlife should live side by side without fear.

1 2 3 4 5 6 7

All living beings are part of one big family.

1 2 3 4 5 6 7

I feel a strong emotional bond with animals.

1 2 3 4 5 6 7

I care about wildlife as much as I do about other people.

1 2 3 4 5 6 7

3. Attitudes

Hyenas

Hyenas should be protected.

1 2 3 4 5 6 7

Hyenas play an important role in nature.

1 2 3 4 5 6 7

Hyenas are important in our culture.

1 2 3 4 5 6 7

Hyenas are fascinating/interesting animals.

1 2 3 4 5 6 7

Hyenas are dangerous to people.

1 2 3 4 5 6 7

Hyenas are dangerous to livestock.

1 2 3 4 5 6 7

Hyenas belong in the Ngorongoro Conservation Area and should be able to live here.

1 2 3 4 5 6 7

Losing livestock to predators is natural and acceptable.

1 2 3 4 5 6 7

The fact that hyenas scavenge on dead, diseased livestock is good for the ecosystem and/or the health of my herd.

1 2 3 4 5 6 7

Management strategies

Using guard dogs is an effective method of protecting livestock.

1 2 3 4 5 6 7

Employing two herd boys instead of just one is an effective method of protecting livestock.

1 2 3 4 5 6 7

Improving boma construction would deter attacks on my livestock.

1 2 3 4 5 6 7

A compensation scheme would make me less likely to kill predators in retaliation.

1 2 3 4 5 6 7

4. Interviewee information

Age: ______
Sex: ______
Number of cattle: ______sheep:______ goats:______donkeys:______
Village: ________________
Profession: __________________

Appendix B: Human-Carnivore Coexistence Questionnaire

Date:
Translator:
Investigator:
Interview ID:
Before or After treatment (circle one)

Introduction: My name is ___________ and I am a researcher with __________. I am studying the Maasai community's relationship with wildlife, especially predators (hyenas, lions, and leopards). I am particularly interested in how the predators are impacting your livelihoods due to predation on livestock and how this affects your perceptions towards predators. Over the next 20-30 minutes, I will ask you a series of questions about your experiences, values, and emotions towards predators, and what sorts of management strategies you would favor. You can take as much time as you need to answer the questions and explain your thoughts. Participation is completely voluntary and all your responses will be confidential. I will take notes on this sheet of paper to record your responses.

1. Depredation

1.1. Livestock loss:

1.1.1. How many cattle, sheep, goats, and donkeys do you lose every year to hyenas?

1.1.2. How many cattle, sheep, goats, and donkeys do you lose every year to lions?

1.1.3. How many cattle, sheep, goats, and donkeys do you lose every year to leopards?

1.1.4. How many cattle, sheep, goats, and donkeys do you lose every year to disease and drought?

1.2. Have you seen any of the predators attack your livestock mentioned above?

Which one(s): ___________________

1.3. Have you or anyone in your family been attacked by a predator mentioned above?

Which one(s): ___________________

2. Wildlife Value Orientations

Domination

2.1. Wildlife is on Earth for people to use.

1 2 3 4 5 6 7

2.2. People can kill wildlife if they think it poses a threat to their life.

1 2 3 4 5 6 7

2.3. The needs of humans are more important than wildlife protection.

1 2 3 4 5 6 7

Mutualism

2.4. I feel a strong emotional bond with wild animals.

1 2 3 4 5 6 7

2.5. I care about wildlife as much as I do about other people.

1 2 3 4 5 6 7

2.6. I take comfort in the relationships I have with wild animals.

1 2 3 4 5 6 7

3. Hyenas

3.1. To what extent do you like or dislike hyenas?

1 2 3 4 5 6 7

3.2. I fear hyenas.

1 2 3 4 5 6 7

3.3. I find hyenas disgusting.

1 2 3 4 5 6 7

3.4. I feel happy about hyenas.

1 2 3 4 5 6 7

3.5. Hyenas should be protected.

1 2 3 4 5 6 7

3.6. Hyenas play an important role in nature.

1 2 3 4 5 6 7

3.7. Hyenas are important in Maasai culture.

1 2 3 4 5 6 7

3.8. It is acceptable that the NCAA kill hyenas to reduce their numbers.

1 2 3 4 5 6 7

3.9. It is acceptable that the NCAA relocate hyenas far away from my village.

1 2 3 4 5 6 7

3.10. It is acceptable that the NCAA leave hyenas in the Ngorongoro Conservation Area.

1 2 3 4 5 6 7

4. Lions

4.1. To what extent do you like or dislike lions?

1 2 3 4 5 6 7

4.2. I fear lions.

1 2 3 4 5 6 7

4.3. I find lions disgusting.

1 2 3 4 5 6 7

4.4. I feel happy about lions.

1 2 3 4 5 6 7

4.5. Lions should be protected.

1 2 3 4 5 6 7

4.6. Lions play an important role in nature.

1 2 3 4 5 6 7

4.7. Lions are important in Maasai culture.

1 2 3 4 5 6 7

4.8. It is acceptable that the NCAA kill lions to reduce their numbers.

1 2 3 4 5 6 7

4.9. It is acceptable that the NCAA relocate lions far away from my village.

1 2 3 4 5 6 7

4.10. It is acceptable that the NCAA leave lions in the Ngorongoro Conservation Area.

1 2 3 4 5 6 7

5. Leopards

5.1. To what extent do you like or dislike leopards?

1 2 3 4 5 6 7

5.2. I fear leopards.

1 2 3 4 5 6 7

5.3. I find leopards disgusting.

1 2 3 4 5 6 7

5.4. I feel happy about leopards.

1 2 3 4 5 6 7

5.5. Leopards should be protected.

1 2 3 4 5 6 7

5.6. Leopards play an important role in nature.

1 2 3 4 5 6 7

5.7. Leopards are important in Maasai culture.

1 2 3 4 5 6 7

5.8. It is acceptable that the NCAA kill leopards to reduce their numbers.

1 2 3 4 5 6 7

5.9. It is acceptable that the NCAA relocate leopards far away from my village.

1 2 3 4 5 6 7

5.10. It is acceptable that the NCAA leave leopards in the Ngorongoro Conservation Area.

1 2 3 4 5 6 7

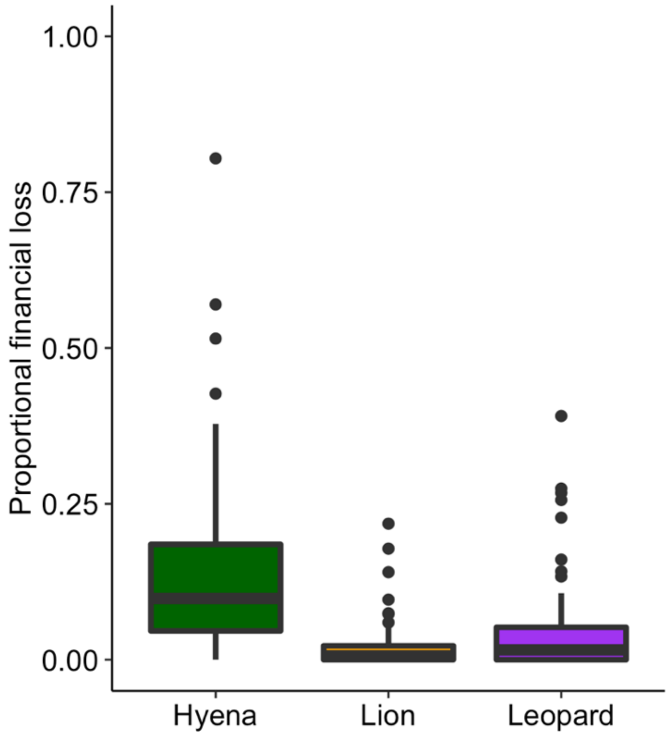
6. Interviewee information

Age: ______
Sex: ______
Number of cattle: ______sheep:______ goats:______donkeys:______
Village: ________________
Profession: __________________

Appendix C: Data on cause of livestock and financial loss

Supplementary Table 1: Mean (± standard error) number of livestock heads killed (column "Heads") and the corresponding financial loss per interviewee caused (in USD; column "Financial") by three species of wild carnivores and by disease/drought. The calculation of means was restricted to cases where the interviewee owned at least one head of cattle (*n* = 99 respondents), sheep (*n* = 99), goat (*n* = 95), or donkey (*n* = 89) prior to losses.

Cause of loss	**Cattle**		**Sheep**		**Goat**		**Donkey**	
	Heads	Financial	Heads	Financial	Heads	Financial	Heads	Financial
Hyena	6.9 ± 0.8	1200.4 ± 139.2	14.0 ± 1.8	672.0 ± 84.2	10.5 ± 1.6	505.8 ± 74.7	3.9 ± 0.5	342.1 ± 47.1
Lion	2.0 ± 0.3	351.5 ± 48.0	0.1 ± 0.1	4.9 ± 3.5	0.1 ± 0.1	3.5 ± 3.5	0.2 ± 0.1	17.6 ± 6.8
Leopard	1.8 ± 0.6	309.3 ± 97.4	4.7 ± 1.2	225.9 ± 55.2	6.7 ± 1.3	319.3 ± 63.5	0.0 ± 0.0	2.0 ± 2.0
Disease/drought	40.6 ± 5.3	7067.2 ± 926.8	31.8 ± 4.1	1528.2 ± 196.0	24.5 ± 3.6	1176.8 ± 172.8	2.3 ± 0.7	200.4 ± 60.6



Supplementary Figure 1: Proportional financial loss due to depredation of livestock by spotted hyenas, lions, and leopards in the Maasai community living in Ngorongoro Conservation Area, Tanzania. Livestock loss was estimated based on the total number of heads of each species of livestock owned by each interviewee (*n* = 100) and on the number of heads that reportedly died. Financial loss was then quantified by converting the number of heads into their estimated financial value on the local market (see methods). Boxes indicate the interquartile range around the median (horizontal bar), vertical bars represent financial losses that lie within 1.5 times the interquartile range. Dots represent data with a value higher than 1.5 times the interquartile range. The mean proportional financial loss due to disease and drought (not depicted) was 38.2% ± 2.3%.

Appendix D: Additional ordinal logistic regression model results

Supplementary Table 2: Variation in acceptance scores by Maasai pastoralists as a function of management strategies, carnivore species, emotions, cultural importance, and livestock depredation. Shown are the odds ratios (OR), their associated 95% confidence intervals ($CI_{95\%}$), and p-values for each predictor, as derived from an ordinal logistic regression model (individual-level random effect variance = 0.07). OR > 1 and OR < 1 indicate a relative increase and decrease, respectively, in the acceptance score associated with a 1-unit increase or shift in the focal predictor when all other covariates are held constant at their population mean or reference level. The reference carnivore species is the hyena and the reference management strategy is relocation. Threshold coefficients refer to the cumulative probability that an acceptance score is at or below the threshold cut point, e.g. the OR for the threshold 2|3 compares the probability of the acceptance score falling within the range of 1-2 to the probability of the acceptance score falling within the range of 3-7. Data in bold were deemed significant ($p < 0.05$).

Predictor	OR	$CI_{95\%}$	*p*
Threshold coefficients			
1|2	0.13	0.08 - 0.22	-
2|3	0.66	0.41 - 1.07	-
3|4	1.07	0.66 - 1.72	-
4|5	2.06	1.27 - 3.35	-
5|6	5.47	3.31 - 9.05	-
6|7	17.92	10.47 - 30.69	-
Management strategies			
No action	**3.19**	**1.68 - 6.05**	**<0.001**
Lethal control	**0.30**	**0.15 - 0.59**	**<0.001**
Species			
Lion	**0.24**	**0.11 - 0.52**	**<0.001**
Leopard	**0.23**	**0.12 - 0.43**	**<0.001**
Emotions			
Joy	0.87	0.73 - 1.03	0.10
Disgust	1.09	0.94 - 1.26	0.25
Fear	1.08	0.97 - 1.20	0.18
Cultural importance	**0.83**	**0.72 - 0.96**	**0.011**
Livestock depredation	**0.01**	**0.00 - 0.13**	**<0.001**
Interaction terms			
No action*Lion	**4.86**	**1.75 - 13.50**	**0.002**

Lethal control*Lion	1.61	0.53 - 4.86	0.40
No action*Leopard	**7.02**	**2.95 - 16.71**	**<0.001**
Lethal control*Leopard	1.26	0.07 - 0.44	0.63
No action*Joy	**1.79**	**1.42 - 2.26**	**<0.001**
Lethal control*Joy	**0.67**	**0.52 - 0.85**	**0.001**
No action*Disgust	0.85	0.70 - 1.03	0.10
Lethal control*Disgust	1.09	0.88 - 1.34	0.44
No action*Fear	1.05	0.82 - 1.10	0.53
Lethal control*Fear	0.85	0.73 - 1.00	0.057
No action*Cultural importance	**1.44**	**1.18 - 1.75**	**<0.001**
Lethal control*Cultural importance	0.96	0.77 - 1.20	0.70
No action*Livestock depredation	**156.20**	**5.40 - 4515.46**	**0.003**
Lethal control*Livestock depredation	34.93	0.97 - 1253.46	0.052

Supplementary Table 3: Variation in acceptance scores by Maasai pastoralists as a function of management strategies, carnivore species, emotions, cultural importance, and livestock depredation. Shown are the odds ratios (OR), their associated 95% confidence intervals ($CI_{95\%}$), and p-values for each predictor, as derived from an ordinal logistic regression model (individual-level random effect variance = 0.07). OR > 1 and OR < 1 indicate a relative increase and decrease, respectively, in the acceptance score associated with a 1-unit increase or shift in the focal predictor when all other covariates are held constant at their population mean or reference level. The reference carnivore species is the hyena and the reference management strategy is lethal control. Threshold coefficients refer to the cumulative probability that an acceptance score is at or below the threshold cut point, e.g. the OR for the threshold 2|3 compares the probability of the acceptance score falling within the range of 1-2 to the probability of the acceptance score falling within the range of 3-7. Data in bold were deemed significant (*p* < 0.05).

Predictor	OR	$CI_{95\%}$	*p*
Threshold coefficients			
1|2	0.44	0.26 - 0.74	-
2|3	2.23	1.34 - 3.73	-
3|4	3.58	2.13 - 6.02	-
4|5	6.90	4.06 - 11.74	-
5|6	18.34	10.55 - 31.89	-
6|7	60.08	33.33 - 108.26	-
Management strategies			
No action	**10.70**	**5.44 - 21.03**	**<0.001**
Relocation	**3.35**	**1.68 - 6.65**	**<0.001**
Species			
Lion	**0.39**	**0.17 - 0.89**	**0.025**
Leopard	**0.29**	**0.15 - 0.57**	**<0.001**
Emotions			
Joy	**0.58**	**0.48 - 0.69**	**<0.001**
Disgust	**1.18**	**1.01 - 1.38**	**0.034**
Fear	0.92	0.81 - 1.04	0.19
Cultural importance	**0.79**	**0.67 - 0.94**	**0.008**
Livestock depredation	0.35	0.03 - 4.63	0.43
Interaction terms			
No action*Lion	**3.03**	**1.04 - 8.81**	**0.042**
Relocation*Lion	0.62	0.21 - 1.88	0.40
No action*Leopard	**5.58**	**2.28 - 13.63**	**<0.001**
Relocation*Leopard	0.80	0.32 - 2.01	0.63

No action*Joy	**2.69**	**2.10 - 3.44**	**<0.001**
Relocation*Joy	**1.50**	**1.17 - 1.93**	**0.001**
No action*Disgust	**0.78**	**0.64 - 0.96**	**0.017**
Relocation*Disgust	0.92	0.75 - 1.14	0.44
No action*Fear	1.12	0.95 - 1.31	0.17
Relocation*Fear	1.17	1.00 - 1.38	0.057
No action*Cultural importance	**1.50**	**1.21 - 1.87**	**<0.001**
Relocation*Cultural importance	1.05	0.84 - 1.31	0.70
No action*Livestock depredation	4.47	0.15 - 131.76	0.39
Relocation*Livestock depredation	0.03	0.00 - 1.03	0.052

Supplementary Table 4: Variation in acceptance scores by Maasai pastoralists as a function of management strategies, carnivore species, emotions, cultural importance, and livestock depredation. Shown are the odds ratios (OR), their associated 95% confidence intervals ($CI_{95\%}$), and p-values for each predictor, as derived from an ordinal logistic regression model (individual-level random effect variance = 0.07). OR > 1 and OR < 1 indicate a relative increase and decrease, respectively, in the acceptance score associated with a 1-unit increase or shift in the focal predictor when all other covariates are held constant at their population mean or reference level. The reference carnivore species is the lion and the reference management strategy is no action. Threshold coefficients refer to the cumulative probability that an acceptance score is at or below the threshold cut point, e.g. the OR for the threshold 2|3 compares the probability of the acceptance score falling within the range of 1-2 to the probability of the acceptance score falling within the range of 3-7. Data in bold were deemed significant ($p < 0.05$).

Predictor	OR	$CI_{95\%}$	*p*
Threshold coefficients			
1|2	0.04	0.02 - 0.06	-
2|3	0.18	0.11 - 0.28	-
3|4	0.28	0.18 - 0.44	-
4|5	0.55	0.36 - 0.84	-
5|6	1.45	0.95 - 2.22	-
6|7	4.75	3.01 - 7.48	-
Management strategies			
Relocation	**0.06**	**0.03 - 0.12**	**<0.001**
Lethal control	**0.03**	**0.02 - 0.06**	**<0.001**
Species			
Hyena	0.85	0.42 - 1.69	0.64
Leopard	1.35	0.79 - 2.31	0.28
Emotions			
Joy	**1.55**	**1.31 - 1.82**	**<0.001**
Disgust	0.92	0.81 - 1.06	0.24
Fear	1.03	0.93 - 1.14	0.59
Cultural importance	**1.19**	**1.04 - 1.36**	**0.013**
Livestock depredation	1.57	0.17 - 14.97	0.70
Interaction terms			
Relocation*Hyena	**4.86**	**1.75 - 13.50**	**0.002**
Lethal control*Hyena	**3.03**	**1.04 - 8.81**	**0.042**
Relocation*Leopard	0.69	0.32 - 1.52	0.36
Lethal control*Leopard	0.54	0.23 - 1.28	0.16

Relocation*Joy	**0.56**	**0.44 - 0.71**	**<0.001**
Lethal control*Joy	**0.37**	**0.29 - 0.48**	**<0.001**
Relocation*Disgust	1.18	0.97 - 1.44	0.10
Lethal control*Disgust	**1.28**	**1.05 - 1.57**	**0.017**
Relocation*Fear	1.05	0.91 - 1.21	0.53
Lethal control*Fear	0.90	0.76 - 1.05	0.17
Relocation*Cultural importance	**0.70**	**0.57 - 0.85**	**<0.001**
Lethal control*Cultural importance	**0.67**	**0.54 - 0.83**	**<0.001**
Relocation*Livestock depredation	**0.01**	**0.00 - 0.19**	**0.003**
Lethal control*Livestock depredation	0.22	0.01 - 6.59	0.39

Chapter 3

Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas

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Detailed contributions:

The original idea to assess the effects of diurnal pastoralism on group-living large carnivores was developed by Oliver Höner (OH). The idea to embed the study within the context of pastoralism and spotted hyena clans in the Ngorongoro Crater was implemented by Arjun Dheer (AD), Eve Davidian (ED), and OH. The cortisol-3-CMO enzyme immunoassay was initially developed by Martin Dehnhard, and was physiologically and biologically validated by Martin Dehnhard, Sarah Benhaiem, Heribert Hofer, and Marion East. The ideas to standardize fecal glucocorticoid metabolite concentrations for long-term studies and to assess aging in fecal samples and hormone extracts were developed by ED. Fecal samples were collected by AD, ED, Philemon Naman (PN), OH, and Bettina Wachter. Socio-demographic and ecological data were collected by AD, ED, PN, Victoria Shayo (VS), OH, and Bettina Wachter. Fecal sample freeze-drying, metabolite extraction, and measurements of concentrations in cortisol metabolites were conducted by AD, ED, Jella Wauters (JW), Mareen Albrecht, Heidrun Barleben, Katrin Paschmionka, and Sylvia Schultz van Endert. Statistical analyses were conceptualized and conducted by AD, ED, JW, Alexandre Courtiol (AC), and Liam Bailey (LB), under the guidance of OH. The manuscript was primarily written by AD, ED, AC, and LB, and edited by JW and OH.

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RESEARCH ARTICLE

Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas

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Abstract

1. Anthropogenic activity can have substantial effects on wildlife. These effects may vary according to the characteristics of the activity and the species involved. Although effects on behaviour are well studied, studies of effects on fitness and physiology are scarce, particularly for group-living species.
2. We exploited a natural experimental setup to investigate the effect of diurnal pastoralism on juvenile recruitment and allostatic load in a population of free-ranging spotted hyenas in the Ngorongoro Crater, Tanzania, over a 24-year period.
3. Pastoralism was restricted to the territories of two of the eight study clans, allowing us to compare juvenile recruitment in exposed and unexposed clans. We also compared faecal glucocorticoid metabolite concentrations (fGMC)—a biomarker of an organism's allostatic load—between exposed and unexposed clans using 975 faecal samples from 475 hyenas.
4. We found no detectable difference in juvenile recruitment nor fGMC between the exposed and unexposed clans, indicating that the pastoralism had no substantial deleterious effect on the spotted hyenas. The lack of a deleterious effect likely stems from the combined effect of the predictable and undisruptive nature of the pastoralism, the socio-ecology of spotted hyenas and the Ngorongoro Crater's consistently abundant prey.
5. Our findings demonstrate that exposure to anthropogenic activity may be compatible with the persistence of certain group-living species, especially if the overlap between the species' critical behaviours and the activity is limited. Our study thereby provides new perspectives for ecologists, conservation biologists and stakeholders who seek to assess human–wildlife conflicts and balance the needs of local human communities and wildlife.

1 | INTRODUCTION

Anthropogenic activity poses challenges for conservation because it can strongly affect wildlife (Beale, 2007) and has become more intense and widespread since the industrial revolution (Lewis & Maslin, 2015). The effects of anthropogenic activity on wildlife may vary greatly, depending on an interaction between its characteristics and the species involved (Tablado & Jenni, 2017). To promote human–wildlife coexistence, it is therefore important to identify which activities are sustainable by quantifying their effects on different species. This evidence-based approach is key for the effective management of protected areas (Watson et al., 2014).

The effects of anthropogenic activity on wildlife behaviour are well documented (Bond et al., 2021; Doherty et al., 2021; Gaynor et al., 2018). In contrast, its effects on fitness traits (e.g. reproductive performance and survivorship) are poorly understood, despite being more salient to population persistence and conservation (López-Bao et al., 2017; Ménard et al., 2014). Similarly, anthropogenic effects on wildlife physiology (e.g. allostatic load) are comparatively not well studied, but may have strong implications for health and survival (Gingery et al., 2021). Changes in behaviour are not always indicative of fitness or physiological effects (Sullivan et al., 2017). For example, exposure to human pedestrians substantially altered space use, but not pup survival, in eastern wolves *Canis lycaon* (Argue et al., 2008). Therefore, detectable changes in behaviour due to anthropogenic activity may not always be of conservation concern. More knowledge of how anthropogenic activity affects fitness and physiology is needed (Beehner & Bergman, 2017).

The effects of anthropogenic activity on fitness may depend on how unpredictable and disruptive of critical behaviours the activity is (Francis & Barber, 2013). If an activity is unpredictable, the ability of animals to habituate is reduced, and thus, fitness costs may increase (Frid & Dill, 2002). For example, bighorn sheep *Ovis canadensis* herds subject to intermittent hiking by humans produced fewer recruits than herds subject to predictable hiking (Wiedmann & Bleich, 2014). Highly disruptive activities are those that greatly impede critical behaviours, which are necessary for reproduction and/or survival (e.g. foraging and offspring care; Broekhuis, 2018). Animals exposed to highly disruptive activities may lose the ability to detect threats, acquire food and find mates; disruptions to these critical behaviours have been associated with fitness costs (Longcore & Rich, 2004). Therefore, the unpredictability and disruptiveness of an activity may determine how conducive it is to human–wildlife coexistence.

The disruptiveness of an anthropogenic activity can also differ between species, depending on the species' biology and social system (Berger-Tal & Saltz, 2016). An activity that takes place during the day is unlikely to be very disruptive to species that conduct critical behaviours at night (Rottstock et al., 2020). For example, diurnal, non-motorized human recreation did not greatly disrupt foraging by nocturnal carnivores (Reilly et al., 2017). In contrast, artificial lighting at night strongly disrupted foraging and migration in nocturnal bats and birds, which resulted in fitness costs (Stone et al., 2009; Winger et al., 2019). Another factor that may influence the disruptiveness of an activity is the social system, in particular the social organization (sensu Kappeler, 2019), that is, whether animals live in groups, in pairs, or solitarily (Rowell, 1993). Group-living, for example, may improve vigilance and defence of food and offspring in response to human presence, which may buffer animals from suffering fitness costs compared to pair-living or solitary counterparts (Gittleman, 2019). Yet, not all group-living species are necessarily affected by anthropogenic activity the same way, due to variations in other aspects of their social system, including their mating system, social structure and care system (sensu Kappeler, 2019). For example, group-living species that are obligate cooperative breeders—a system in which 'helpers' provide offspring care—may be particularly susceptible to extinction from anthropogenic activities if group size is reduced (Angulo et al., 2013; Clutton-Brock, 2021). Yet, these effects have rarely been tested. Scientists can seldom complete studies of multiple social groups, due to immense financial, logistical and temporal demands, which may limit the generalizability of findings (Moss et al., 2011). Furthermore, such studies on large-bodied, long-lived species such as large carnivores are critically lacking. Large carnivores not only provide key ecosystem services, but are often implicated in human–wildlife conflict (Dheer et al., 2021; Nyhus, 2016), so understanding how they can coexist with humans is particularly important.

We used a natural experiment to study the effect of pastoralism—a globally widespread anthropogenic activity—on a population of free-ranging spotted hyenas *Crocuta crocuta* (henceforth 'hyenas') resident on the floor of the Ngorongoro Crater, Tanzania. The population has been the subject of a long-term study since 1996 (Höner et al., 2022). Hyenas are apex predators, crucial components of ecological communities across sub-Saharan Africa, and live in non-cooperative breeding, hierarchical (i.e. ranked) social groups called 'clans' (Davis et al., 2022; Frank, 1986). Critical behaviours (e.g. foraging and suckling) in hyenas mostly occur at night or dawn and dusk (Holekamp et al., 1997; Kruuk, 1972), although very young cubs are also regularly suckled during the day (Hofer et al., 2016; Wachter et al., 2002). Hyenas are behaviourally flexible; previous research suggests that they can greatly adjust their behaviour—for example, shifting den attendance and suckling bouts to nighttime—in response to diurnal pastoralism (Boydston, Kapheim, Szykman, et al., 2003; Kolowski et al., 2007). Yet, whether diurnal pastoralism affected fitness-related traits or physiology remains unknown.

The pastoralism we studied occurred from 1996 to 2016 (Melubo & Lovelock, 2019). It was restricted to the territories of two of the eight Crater clans (Figure 1), creating a natural experiment that allowed us to compare 'exposed' and 'unexposed' clans over an extended period of time. We assessed the effect of pastoralism on juvenile recruitment—estimated by the survival of cubs to 12 months—for an integrative comparison of fitness (Chesson, 2003). Our long-term data collection allowed us to quantify the effect of pastoralism while accounting for natural variations in recruitment through space and time. To disentangle the effects of pastoralism from those of other socio-ecological parameters, we accounted for disease outbreaks, the number of adult females in a clan, pressure from the main interspecific competitor (sightings of lions; *Panthera leo*), and prey availability (number of preferred prey animals) in the given clan territory. Previous research has associated these covariates with fitness-related traits in hyenas (Höner et al., 2005, 2006; Trinkel et al., 2004; Watts & Holekamp, 2008).

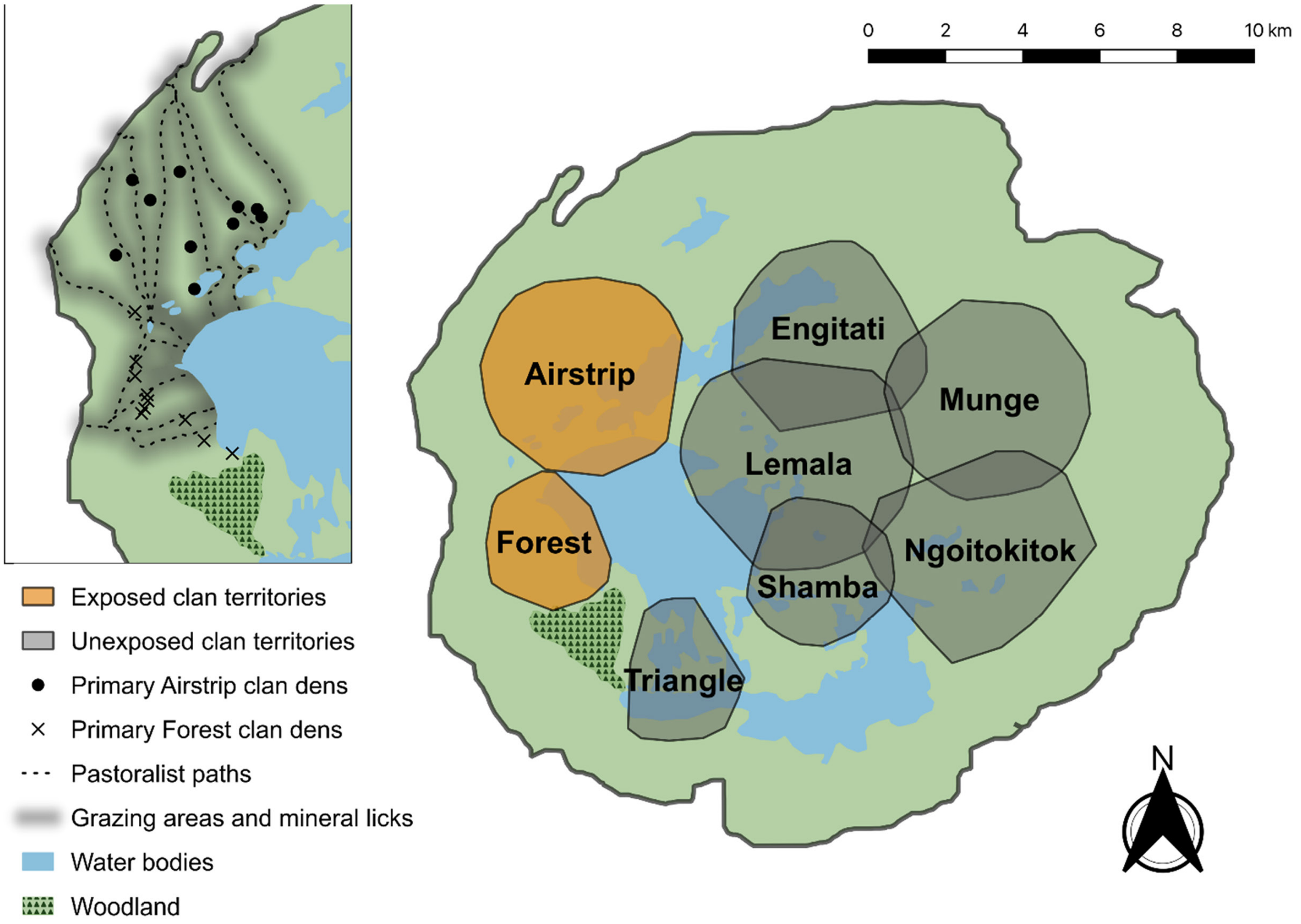

FIGURE 1 Hyena clan territories, primary clan dens, pastoralist paths, grazing areas and mineral licks in the Ngorongoro Crater. Territory boundaries are based on 85% minimum convex polygons (MCPs) of adult female hyena sightings from 1996 to 2019 for each clan. MCPs of 85% were chosen to accurately represent the locations of clan territories across the study period. Clan territories are colour coded based on whether or not they were exposed to pastoralism from 1996 to 2016. Territories are labelled with corresponding clan names. The inset depicts the primary dens ($n = 20$) that the exposed clans used from 1996 to 2016 and the major paths, grazing areas and mineral licks that Maasai and their livestock used from 1996 to 2016

Because the pastoralism we studied was diurnal, it was unlikely to affect foraging, but likely led to more nocturnal den attendance and suckling of young cubs (Kolowski et al., 2007). Such changes may also have increased the risk of hyenas being killed by lions, which are nocturnal (Cozzi et al., 2012). Thus, we predicted that exposed clans would produce fewer juvenile recruits than unexposed clans would.

Furthermore, to assess the effect of pastoralism on allostatic load, we compared the concentration of faecal glucocorticoid metabolite concentrations (fGMC) in hyenas from exposed and unexposed clans. Glucocorticoids are mediators of endocrine mechanisms that regulate essential biological functions (McEwen & Wingfield, 2003). Chronically elevated fGMC can occur as a response to repeated exposure to challenges, which may prevent an individual from adequately responding to subsequent challenges (Bonier et al., 2009). Thus, we predicted that if pastoralism led to chronically elevated allostatic load, then hyenas from exposed clans would have higher fGMC than those from unexposed clans.

2 | MATERIALS AND METHODS

2.1 | Study area and population

This study took place in the Ngorongoro Crater (3°11′S, 35°34′E), a volcanic caldera located in the wider Ngorongoro Conservation Area (NCA), Tanzania, part of the greater Serengeti ecosystem. The NCA is a multi-use protected area that was established in 1959 and is a United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site with a mandate to protect the interests of wildlife and local human communities (Charnley, 2005). The NCA is inhabited by the Maasai tribe, a semi-nomadic, pastoralist ethnic group traditionally ranging from central Kenya to southern Tanzania (Fratkin, 2001). The Maasai and their livestock resided in the Crater until 1974, when they were evicted and required to live in other parts of the NCA (Moehlman et al., 2020). They were still allowed to enter the Crater to conduct diurnal pastoralism until it was banned at the end of 2016 (Melubo & Lovelock, 2019).

In our study, diurnal pastoralism overlapped with the territories of two of the Crater's eight resident hyena clans from 1996 to 2016 (Figure 1). The pastoralism involved Maasai community members accompanying their livestock—primarily cattle—on designated paths in and out of the Crater. They were required to enter after sunrise and depart before sundown (Musiba & Mabulla, 2010). We tested for fitness and physiological effects of pastoralism by comparing exposed (Airstrip and Forest clans from 1996–2016) and unexposed clans (Engitati, Lemala, Munge, Ngoitokitok, Shamba, and Triangle clans from 1996 to 2016, and all eight clans from 2017 to 2019). Over the same period, the cattle population in the NCA grew from under 120,000 to over 240,000 and the human population from under 43,000 to over 100,000 (Manzano & Yamat, 2018).

2.2 | Data collection

Collection of demographic, behavioural and ecological data occurred between April 1996 and December 2019, on a near-daily basis between 06:00 and 19:00. We recognized individuals based on their pelage patterns, ear notches, scars and other traits. Ages were estimated based on pelage, body size, behaviour and locomotion of cubs, with an accuracy of ±7 days (Pournelle, 1965). For data filtering, cubs were defined as individuals <12 months old, juveniles as individuals 12 to <24 months old and adults as individuals ≥24 months old. The time period between the last sighting in our analyses (31 October 2019) and the last sighting in our database used to inform the analyses (09 July 2021) was 617 days. Individuals not sighted during this period were considered dead. The potential error resulting from this assumption is small because during our study period, only 2.5% of hyenas (n = 53 of 2096) were re-sighted after a 617-day absence. Sexes were identified through observation of external genitalia as described in Frank et al. (1990). Faecal samples were collected opportunistically, immediately after defecation by identified individuals. The study was conducted under research permits 2018-38-NA-90-48 and 2019-20-NA-90-45 issued by the Tanzania Commission for Science and Technology and did not require ethics approval.

2.3 | Juvenile recruitment

Juvenile recruitment in a given clan was defined as the number of cubs born into the clan within a given season (6-month period) that were still alive 12 months later. We chose a 12-month cut-off because mortality substantially decreases after 12 months (Hofer & East, 1995). Seasons were divided into 'dry' and 'wet' according to typical local rainfall patterns: dry seasons were the 6-month period from May 1st through October 31st of each calendar year and wet seasons were those from November 1st through April 30th of the following year (Brandell et al., 2021). We used the sequence of the seasons to test for temporal autocorrelation.

2.4 | Social rank

Individual social rank is an important determinant of various behavioural, reproductive and physiological traits in hyenas (Hofer & East, 2003; Höner et al., 2010). Ordinal ranks were determined based on the history of recorded agonistic interactions and our knowledge of rank inheritance and social queuing (for details, see Davidian et al., 2021). We converted the ordinal rank ($OrdRank_i$) of an individual (i) into a proportional rank ($PropRank_i$) bounded between −1 (bottom rank) and 1 (top rank), accounting for clan size N, using the following formula:

$$PropRank_i = \frac{N - OrdRank_i}{\frac{N-1}{2}} - 1.$$

2.5 | Disease outbreaks

Outbreaks of disease caused by pathogenic *Streptococcus* bacteria occurred multiple times over the course of the long-term study and have been significant sources of mortality in the Ngorongoro Crater hyena population (Höner et al., 2012). Therefore, seasons were categorized as being either outbreak or non-outbreak. The classification depended on whether there were observable clinical signs of *Streptococcus* infection in at least five individual hyenas during the season. Outbreak seasons (n = 5 seasons [3 dry and 2 wet], or 39 clan-seasons) were also associated with a mean 9% decline in total Crater hyena population compared to the preceding season, validating our criterion.

2.6 | Clan territories

We calculated clan territories based on minimum convex polygons (MCP) of adult female sightings. Each territory was characterized by fidelity to the focal clan of ≥90% (i.e. ≥90% of sightings of Crater clan adult females within a given territory were from adult female members of the focal clan). Thus, the percentages used for the MCP varied (Table S1) according to the largest area that still allowed for ≥90% fidelity to the focal clan. We contend this is a more biologically relevant approach than assigning a single MCP percentage for all clans, because it shows accurate variable space use and is rooted in observed behaviour. We divided clan territories into two temporal groups: period 1 (pre-2012) and period 2 (2012–2019), due to changes in prey per capita and clan territory sizes and locations in 2012 (Figures S1 and S2) that may have resulted from changes in vegetation due to a nearby volcanic eruption (De Schutter et al., 2015). A summary of the different MCP used for each clan in periods 1 and 2 is in Table S1. We did not split our territory calculations further because long periods of time were needed to have sufficient sample sizes to calculate accurate territories.

2.7 | Number of adult females

To account for the positive effect of the number of adult females on the total number of juvenile recruits in a given clan, we calculated the number of adult females for each clan-season combination. This was done by counting the maximum number of living adult female clan members at any point within the given 6-month season in the focal clan. For example, if a clan's maximum number of living adult female clan members during a given 6-month season was 20, they were allocated 20 adult females for that clan-season.

2.8 | Lion index

To estimate the competitive influence of lions *Panthera leo*, we created a lion index for each clan-season. We did so by attributing sightings of lions of any age and sex class to the clan territories using GPS coordinates (Garmin GPSMAP 64) and then dividing the obtained number of lion sightings by the corresponding number of adult female hyenas, from the given clan, seen in the clan territory during the given season. To avoid potential inaccuracies in the lion index caused by seasons with reduced observation effort, we only computed this index for seasons in which ≥50% of a clan's adult females were seen. For example, if only three adult females from a clan were seen during a given season, but we knew based on genetic data and sightings from subsequent seasons that the clan had 10 adult females during the given season, we deemed the lion index unreliable and excluded the entire clan-season from our analyses. Out of 384 clan-seasons, 45 had an observation effort of <50%, so we excluded them from our analyses.

2.9 | Prey per capita

We calculated prey per capita for each clan-season combination using data from the bi-annual Crater wildlife census, conducted by the Ngorongoro Conservation Area Authority (NCAA). Censuses fell within the defined seasons from our dataset. We summed counts of individuals from the five prey species most commonly eaten by hyenas in the Crater—blue wildebeest *Connochaetes taurinus*, plains zebra *Equus quagga*, African buffalo *Syncerus caffer*, Grant's gazelle *Nanger granti* and Thomson's gazelle *Eudorcas thomsonii* (Höner et al., 2002)—and divided the counts by the corresponding number of adult female hyenas in the clan during that season. Because the NCAA uses census blocks (Runyoro et al., 1995) that are not fully congruent with clan territories, we used the percentage overlap of census blocks with a given territory to allocate prey. For example, if a census block contained 100 prey animals, and 50% of the census block area overlapped with a clan's territory, then the clan was allocated 50 of the 100 prey animals. There were 10 seasons, that is, 80 clan-seasons, we could not calculate prey per capita for because the NCAA did not conduct censuses. Of those 80 clan-seasons, we had already removed seven from our analyses, because they did not meet our observation effort criterion for the lion index. Thus, we further removed 73 clan-seasons due to missing prey per capita. Our final juvenile recruitment data, therefore, consisted of 266 clan-seasons spread across 38 seasons.

2.10 | Immunoassay protocol

We assessed the physiological costs of pastoralism on hyenas using non-invasive measurements of fGMC. We collected 975 faecal samples from 475 (juvenile or adult) hyenas; 315 samples from 211 females and 660 samples from 264 males. Of these, 88 were from members of exposed clans and 887 from members of unexposed clans. Following collection, faeces were mechanically mixed, subsampled, stored in liquid nitrogen and then transported to the laboratory in Berlin, Germany, on dry ice where they were stored at −80°C until processed for analyses. Samples were freeze-dried before steroid extraction (see Benhaiem et al., 2012; Davidian et al., 2015 for the detailed extraction procedure). The fGMC were measured using an in-house, competitive Enzyme-Linked ImmunoSorbent Assay (ELISA) based on an antibody developed for cortisol-3-CMO previously validated analytically, physiologically and biologically for hyenas (Benhaiem et al., 2012). Measurements were performed in duplicates and deemed reliable when falling within the range of metabolite concentration for which the calibration curve is approximately linear (1.5–25 ng/g of dry faecal matter) and when their coefficient of variation (CV) was <5%.

Faecal extracts were assayed in two batches by the same technician. One batch was run in 2013 (n = 768 extracts, 23 plates) and another in 2020 (n = 207 extracts, 19 plates; Figure S3). Stability of ELISA accuracy and intra- and inter-assay precision were quantified using the CV of repeated measurements of faecal control pools with relatively low and high concentrations; for all pools, intra- and inter-assay CV met the <5% and <20% acceptance criteria (for more details, see Supporting Information). To ensure comparability of the fGMC between the two batches, we applied an established standardization method—as developed in Davidian et al. (2015)—and conducted a quality control assessment of key parameters of assay performance, such as parallelism, analytical precision and quantitative resolution (Table S2; Figure S4). We further exploited our setup to assess the possible deterioration and impact on fGMC of steroids in freeze-dried faecal samples and extracts that were stored at −80°C for 7 years (see Supporting Information and Figure S5).

2.11 | Statistical analyses

We conducted all statistical analyses in R software 4.2.0 (R Core Team, 2022). Data are presented as means ± *SD*, unless stated otherwise. The threshold for statistical significance was set to $\alpha = 0.05$. To test our predictions, we fitted two generalized linear mixed-effects models (GLMMs) using the 'fitme' function from package 'spaMM' (version 3.9; Rousset & Ferdy, 2014): one for juvenile recruitment and one for fGMC. *p*-values for each covariate were calculated using likelihood ratio tests for which the distribution of the test statistic under the null hypothesis was computed using 999 parametric bootstrap replicates. Model assumptions were evaluated and affirmed using package 'DHARMa' version 0.4.4 (Hartig, 2021).

We computed predictions associated 95% confidence intervals from the GLMM for each statistically significant independent variable and exposure category using the function 'pdep_effects' in 'spaMM'. For ease of interpretation, we calculated the percent change in the absolute value of juvenile recruitment and fGMC resulting from a one-unit change in the value of the focal predictor compared to its reference, calculated as [exp(coefficient) − 1]*100.

2.11.1 | Juvenile recruitment

We tested the effect of pastoralism (qualitative, two levels: exposed or unexposed), outbreaks (qualitative, two levels: yes or no), the number of adult females (quantitative), the lion index (quantitative) and prey per capita (quantitative) for each clan-season on the number of juvenile recruits per clan using a negative binomial GLMM fitted to the data. We chose the negative binomial family because the dependent variable was a non-negative integer and the goodness of fit for this model was better than that of a Poisson family on our data. These two distributions are the two main alternatives used to fit discrete quantitative data. We used the logarithm as the link function. We also applied a natural log transformation to the number of adult females for improved goodness of fit. The clan identity ($n = 8$) and the season ($n = 38$) were treated as random effects. We modelled possible temporal autocorrelation in the models by allowing for covariation between the successive realizations of the random effect 'season' (AR1 structure). We also performed likelihood ratio tests comparing model fits, considering either the presence or absence of interactions between exposure and all other covariates. We retained the model without interactions following the principle of parsimony, because there was no detectable improvement in likelihood after considering interactions ($\chi^2 = 2.02$, $df = 4$, $p = 0.72$; Table S3).

2.11.2 | fGMC

We tested the effect of pastoralism, age (quantitative, continuous number in years), clan size (quantitative, total number of hyenas in the clan, inclusive of all sexes, ages and ranks), and proportional rank (quantitative, range from −1 to 1), on natural log-transformed fGMC using a gamma GLMM fitted to the data. We chose the gamma family because the dependent variable was non-negative and continuous. We used the logarithm as the link function. The hyena's identity ($n = 475$) and the season ($n = 41$) were treated as random effects. We used 41 of the possible 48 seasons because faecal samples were not collected during 7 seasons. All covariates were accurate to the day of sample collection, for example, the proportional rank associated with a given fGMC was the defecating hyena's proportional rank on the day of sample collection. We modelled the possible temporal autocorrelation as previously described. As with recruitment, we performed likelihood ratio tests comparing model fits considering either the presence or absence of interactions between the exposure predictor and all other covariates. We again retained the model without interactions, because there was no detectable difference in likelihood after considering interactions ($\chi^2 = 0.28$, $df = 3$, $p = 0.98$; Table S4).

3 | RESULTS

3.1 | Effects of pastoralism and ecological covariates on juvenile recruitment

Exposed clans produced more juvenile recruits per season (4.46 ± 3.85 juveniles, $n = 56$ seasons) than unexposed clans did (3.50 ± 3.11 juveniles, $n = 210$ seasons), though the difference was not detectable (Mann–Whitney *U* test; $U = 6798.5$, $p = 0.071$; Figure 2a). A GLMM confirmed that there was no detectable difference in predicted juvenile recruitment between exposed (4.27 juveniles; CI 95% = 2.68–6.83) and unexposed clans (3.50 juveniles, CI 95% = 2.35–5.23; Figure 3a) when controlling for other covariates (see Table 1 for detailed model coefficients). There were detectable effects of outbreaks (negative), number of adult females (positive) and lion index (positive) on juvenile recruitment (Table 1). The predicted number of juvenile recruits produced by clans during outbreak seasons was 2.59 (CI 95% = 1.61–4.18); during non-outbreak seasons, it was 3.86 (CI95% = 2.63–5.68; Figure 3b). A one-unit increase in the number of adult females on the natural log scale (=32.03 real females for one log unit above the average number of adult females, 18.64 ± 10.52) led to a predicted 136.3% increase in the number of juvenile recruits (Figure 3c). A one-unit increase in the lion index (i.e. one additional lion sighting per adult female hyena seen) led to a predicted 6.5% increase in the number of juvenile recruits (Figure 3d). The effect of prey per capita was small and not detectable (Table 1).

There was no detectable difference in the number of adult females between exposed (mean = 19.75 ± 10.37, $n = 56$) and unexposed (18.35 ± 10.56, $n = 210$, $U = 6425.5$, $p = 0.29$; Figure S6) clans. The lion index was lower in exposed clan territories (mean = 1.00 ± 1.50, $n = 56$) than in unexposed clan territories (1.70 ± 2.13, $n = 210$; $U = 4586$, $p = 0.011$; Figure 2b), representing a difference of 0.70 lion sightings per adult female hyena seen. In contrast, prey per capita was higher in exposed (102.79 ± 86.11, $n = 56$) than unexposed clan territories (84.07 ± 87.81, $n = 210$; $U = 7294$, $p = 0.006$; Figure 2c).

3.2 | Effects of pastoralism and socio-ecological covariates on fGMC

There was a biologically small but near-detectable difference in observed fGMC between exposed clans (mean = 50.98 ± 63.56 ng/g,

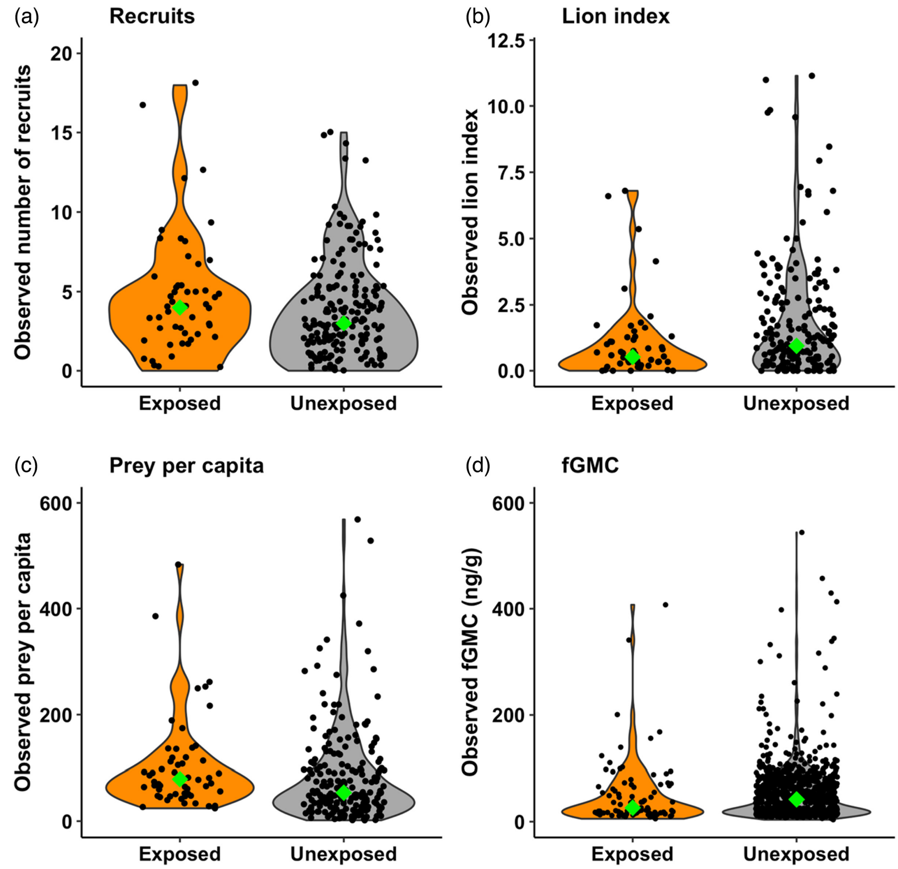

FIGURE 2 Observed ecological data pertaining to hyena clans. (a) Number of juvenile recruits, (b) lion index, (c) prey per capita, and (d) faecal glucocorticoid metabolite concentration (fGMC). Each violin plot displays the distribution of data for the respective clan category (exposed or unexposed to pastoralism). Exposed clans (orange) were subject to pastoralism while unexposed clans (grey) were not. Black dots represent observed data after horizontal jittering was applied for ease of visualization. Green diamonds represent sample medians

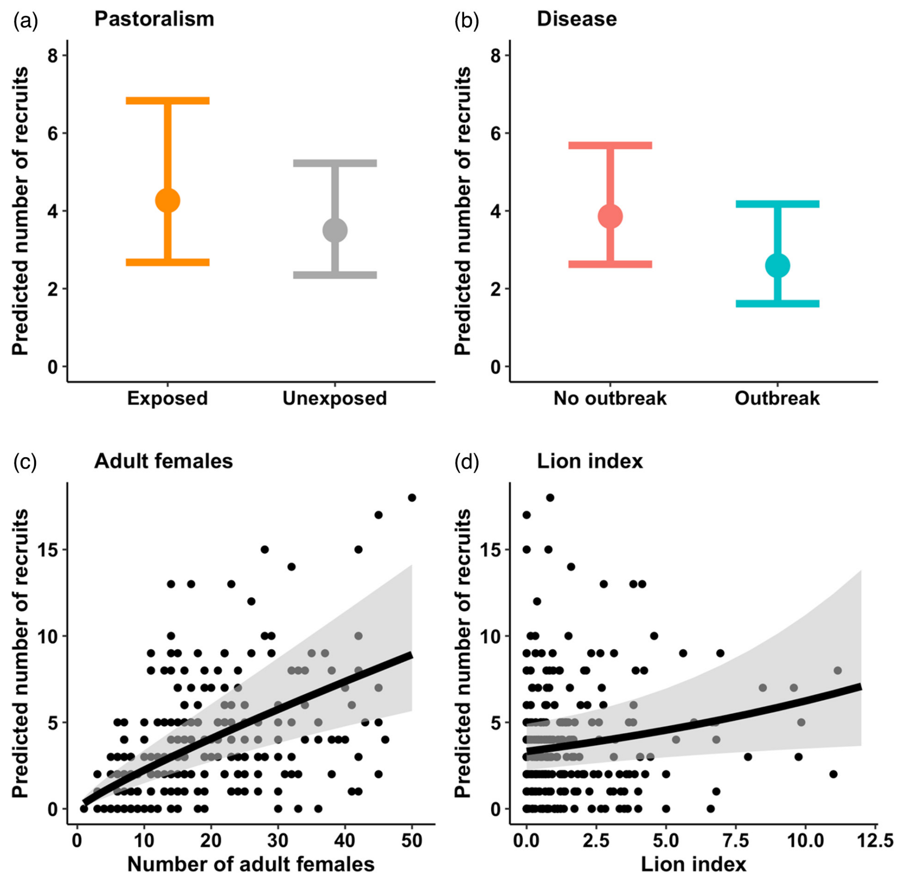

FIGURE 3 Effect of anthropogenic activity and ecological covariates on the predicted number of juvenile recruits in hyena clans. (a) Pastoralism, (b) disease, (c) number of adult females, and (d) lion index. Black dots represent observed data points. Plotted predictions show changes in the response variable given changes in a focal (fixed-effect) variable, computed as the average of predicted values (on the response scale) over the empirical distribution of all other fixed-effect variables and of inferred random effects. This method allows for the visualization of the effect of the given fixed-effect variable while avoiding any effects caused by association between the focal variable and other predictor variables

TABLE 1 Effects of anthropogenic activity and ecological covariates on the number of juvenile recruits in hyena clans. Covariates consist of anthropogenic activity (pastoralism), disease outbreaks, number of adult females, lion index and prey per capita on the number of juvenile recruits produced by hyena clans in the Ngorongoro Crater, Tanzania. The intercept for the model corresponds to the exposed category of hyena clans (subject to pastoralism) and no disease outbreak, with the number of adult females, lion index and prey per capita held at 0. The column 'S.E.' provides standard errors on parameter estimates. The column '% change' gives the percent change in the absolute value of the response variable resulting from a one-unit change in the value of the focal predictor compared to its reference. The column 'L.R.' and '*p*' give, respectively, the likelihood ratio statistics and the *p*-value associated with the likelihood ratio test. Data in bold were deemed statistically significant. Results are based on a negative binomial generalized linear mixed-effects model (GLMM; *p*-values based on a likelihood ratio test using 999 parametric bootstrap replicates). Random variances were estimated for time- ($n = 38$ seasons) and clan-level ($n = 8$ clans) at 0.03. The coefficient for the temporal autocorrelation (AR1 structure) between consecutive seasons was estimated to 0.58

	Estimate	S.E.	% change	L.R.	*p*
Intercept	−1.20	0.36			
Unexposed	−0.20	0.17	−18.0	0.92	0.35
Outbreak	**−0.40**	**0.17**	**−32.8**	**4.07**	**0.043**
Adult females	**0.86**	**0.11**	**136.3**	**28.87**	**0.001**
Lion index	**0.06**	**0.03**	**6.5**	**4.42**	**0.036**
Prey per capita	0.00	0.00	0.1	1.43	0.25

TABLE 2 Effects of anthropogenic activity and socio-ecological covariates on faecal glucocorticoid metabolite concentration (fGMC) in hyenas. Covariates consist of anthropogenic activity (pastoralism), age, clan size and proportional rank on the natural log of the fGMC of hyenas in the Ngorongoro Crater, Tanzania. The intercept for the model corresponds to the exposed category of hyena clans (subject to pastoralism), with age, clan size and proportional rank held at 0. Data in bold were deemed significant. Results are based on a gamma generalized linear mixed-effects model (GLMM; *p*-values based on a likelihood ratio test using 999 parametric bootstrap replicates). Random variances were estimated for time- ($n = 41$ seasons) and individual-level ($n = 475$ hyenas) at 0.003 and 0.005, respectively. The coefficient for the temporal autocorrelation (AR1 structure) between consecutive seasons was estimated to 0.55. See Table 1 legend for details on column names

	Estimate	S.E.	% change	L.R.	*p*
Intercept	1.15	0.04			
Unexposed	0.01	0.03	0.5	0.04	0.85
Age	**0.02**	**0.00**	**1.5**	**37.56**	**0.001**
Clan size	0.00	0.00	0.0	0.11	0.74
Rank	0.01	0.01	1.3	0.83	0.34

$n = 88$ faeces) and unexposed clans (55.09 ± 62.61 ng/g, $n = 887$ faeces; $U = 34{,}167$; $p = 0.054$; Figure 2d). A GLMM revealed no detectable difference in predicted fGMC between exposed and unexposed clans after controlling for other covariates (Table 2). The predicted fGMC for hyenas in exposed clans was 36.32 ng/g (CI 95% = 22.94–61.57 ng/g) and in unexposed 37.01 ng/g (CI 95% = 24.01–60.59 ng/g). The GLMM also revealed that age had a weak, positive effect on fGMC (Table 2); a 1-year increase in age led to the predicted fGMC (i.e. ng/g) increasing by 1.5%. Clan size and rank had small, non-detectable effects on predicted fGMC (Table 2).

4 | DISCUSSION

In this study, we investigated how diurnal pastoralism affected juvenile recruitment and allostatic load in free-ranging hyenas. We used a natural experiment to compare hyena clans exposed and unexposed to pastoralism over the course of 24 years. Exposure to pastoralism did not substantially reduce juvenile recruitment nor elevate fGMC in the hyenas. Three main, non-mutually exclusive scenarios may explain our results.

First, the pastoralism may not have been unpredictable or disruptive enough to reduce juvenile recruitment. Pastoralism occurred predictably, on the same designated paths in and out of the Crater. Its consistency may have allowed hyenas in exposed clans to habituate. The fact that the pastoralism was diurnal may also have made it largely undisruptive to critical behaviours such as foraging and suckling. Hyenas that undertake most of their foraging at night, dawn and dusk (Kruuk, 1972) would have limited overlap with pastoralism. The suckling of young cubs may take place during the day, but previous research showed that hyenas can shift suckling to nighttime to reduce overlap with diurnal pastoralism (Kolowski et al., 2007). Additionally, hyenas readily shift dens following disturbances (Périquet et al., 2015), which allows young cubs to safely suckle. This spatial separation may not have been an option for hyenas in our study, though, due to the small Crater clan territories and the large extent of the pastoralist paths. Our study suggests that spatiotemporal adjustments are not costly enough to reduce juvenile recruitment. Additionally, they indicate that behavioural plasticity may allow hyenas to persist in areas with diurnal anthropogenic activity (Frank & Woodroffe, 2001). Behavioural plasticity may also partly explain why fGMC did not greatly differ between exposed and unexposed clans. Previous research has suggested that hyenas may adjust their behaviour to minimize exposure to social challenges and downregulate their fGMC (Davidian et al., 2021). Thus, hyenas in exposed clans could have made behavioural adjustments, thereby levelling their fGMC to those of hyenas in unexposed clans. Altogether, our results support those of other studies which suggested that predictable, undisruptive activities are conducive to human–wildlife coexistence.

Second, the hyena social system may have buffered exposed clans from the potential negative effects of pastoralism. Hyena clans are hierarchical and have rank-related reproductive skew: low-ranking females have lower reproductive success than high-ranking ones do (Hofer & East, 2003; Holekamp et al., 1996).

Thus, even if the reproductive performance of low-ranking females is greatly reduced, the clan itself may persist. Low-ranking hyenas also have less access to preferred dens and resting areas (e.g. those further away from pastoralist paths) than high-ranking hyenas do (Boydston, Kapheim, Watts, et al., 2003). Accordingly, low-ranking hyenas in exposed clans therefore may have experienced more direct and stronger effects of pastoralism than their high-ranking counterparts did. But because low-ranking females produce fewer recruits a priori, the early loss of few low-ranking cubs may not be noticeable at the group level, allowing the clan to persist. Additional studies conducted at the individual level may detect if low-ranking females indeed buffer the negative effects of anthropogenic activity.

Third, the Crater's consistently high prey abundance (Moehlman et al., 2020) may have buffered any negative effects of pastoralism. Prey-rich environments such as the Crater allow female hyenas to produce sufficient milk for daily suckling and provide favourable early-life conditions (Wachter et al., 2002), which may facilitate juvenile recruitment. In exposed clans, even if pastoralism forced critical behaviours such as suckling to become more nocturnal, the relative ease of acquiring food may have reduced the cost of such adjustments. Furthermore, over the course of our study, the hyena population was recovering from a major decline (Höner et al., 2005) and therefore likely experienced little competition for prey. Consistently abundant prey may also explain why there was no detectable effect of prey per capita on juvenile recruitment, in stark contrast to other studies (Broekhuis et al., 2021; Mills & Harris, 2020). Even if prey per capita within a clan territory declined greatly, there would be plentiful prey in other clan territories that hyenas could access by intruding (Höner et al., 2005). Thus, the Crater's consistently abundant prey may have allowed for coexistence between pastoralism and hyenas.

Among the other covariates in this study, the lion index and the number of adult females had positive effects and outbreaks a negative effect on juvenile recruitment. One explanation for the effect of the lion index is that it may indicate favourable ecological conditions for hyenas, as the two species occupy very similar niches (Davidson et al., 2019; Périquet et al., 2015). Thus, clan-seasons with high lion indices may have had conditions that facilitated juvenile recruitment. A second explanation is that food provisioning by lions for hyenas may have boosted juvenile recruitment. A previous study in the Crater found that dominance between the two species at carcasses is relatively balanced, depending on the hyena-to-lion ratio and the presence of male lions (Höner et al., 2002). The study also found that klepto-parasitism and scavenging by hyenas increased when lion abundance increased. Clans may thus have enjoyed greater access to food (and subsequently, higher juvenile recruitment) when there was a high lion index. The detectable effects of the number of adult females and outbreaks on juvenile recruitment are consistent with previous findings (Green et al., 2019; Höner et al., 2012). Similarly, the detectable positive effect of age on fGMC supports the results from previous studies of hyenas and other mammals (Davidian et al., 2021; Hämäläinen et al., 2015). Evidently, other socio-ecological parameters in our study influenced juvenile recruitment and fGMC much more strongly than pastoralism did. This again suggests that pastoralism had no substantial deleterious effect on the Ngorongoro Crater hyena population.

Although anthropogenic activity is often considered inherently bad for wildlife, its effects may vary according to the type of activity occurring, the focal species' biology and social system, and food availability. Our findings demonstrate that exposure to anthropogenic activity may be compatible with the persistence of certain group-living species, especially if overlap between the species' critical behaviours and the activity is small. This result provides important insights for stakeholders and conservation biologists who seek to balance the needs of local human communities and wildlife. Our study also illustrates that changes in anthropogenic activity represent natural experiments that can be exploited to assess the effects of humans on wildlife. To best distinguish the effect of localized anthropogenic activity from that of larger environmental patterns, such changes in anthropogenic activity must be restricted to specific time periods and locations within a broader monitored area, as is the case in this study. More studies that collectively span a variety of anthropogenic activities, species and social systems—and that quantify anthropogenic effects on fitness and physiology—are needed for effective evidence-based conservation. With a growing number of such studies, it will soon be possible to perform comparative analyses to generate the knowledge needed optimize human–wildlife coexistence.

AUTHOR CONTRIBUTIONS

Arjun Dheer, Eve Davidian, Alexandre Courtiol, Liam D. Bailey and Oliver P. Höner conceived the ideas and designed the methodology; Arjun Dheer, Eve Davidian, Jella Wauters, Philemon Naman, Victoria Shayo and Oliver P. Höner collected the data; Arjun Dheer, Alexandre Courtiol and Jella Wauters analysed the data; Arjun Dheer led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.dv41ns226 (Dheer et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supporting Information

Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas

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Table of Contents

A. Changes in prey distribution in the Ngorongoro Crater

The Ngorongoro Crater was divided into six census blocks (~40 km^2 each) in 1963 to conduct bi-annual, total count wildlife censuses (Moehlman et al., 2020; Runyoro et al., 1995; Figure S1). There was a westward shift in the distribution of preferred hyena prey species between the census blocks in 2012 (Figure S2); prey shifted from census blocks 2, 3, 4, and 5 (henceforth 'east blocks') to census blocks 1 and 6 (henceforth 'west blocks'). Hyena clan territories followed this shift. We therefore opted to divide our clan territory calculations into two periods: period 1 (1996-2012) and period 2 (2012-2019), to reflect changes in prey distribution and subsequent changes in clan territory locations and sizes.

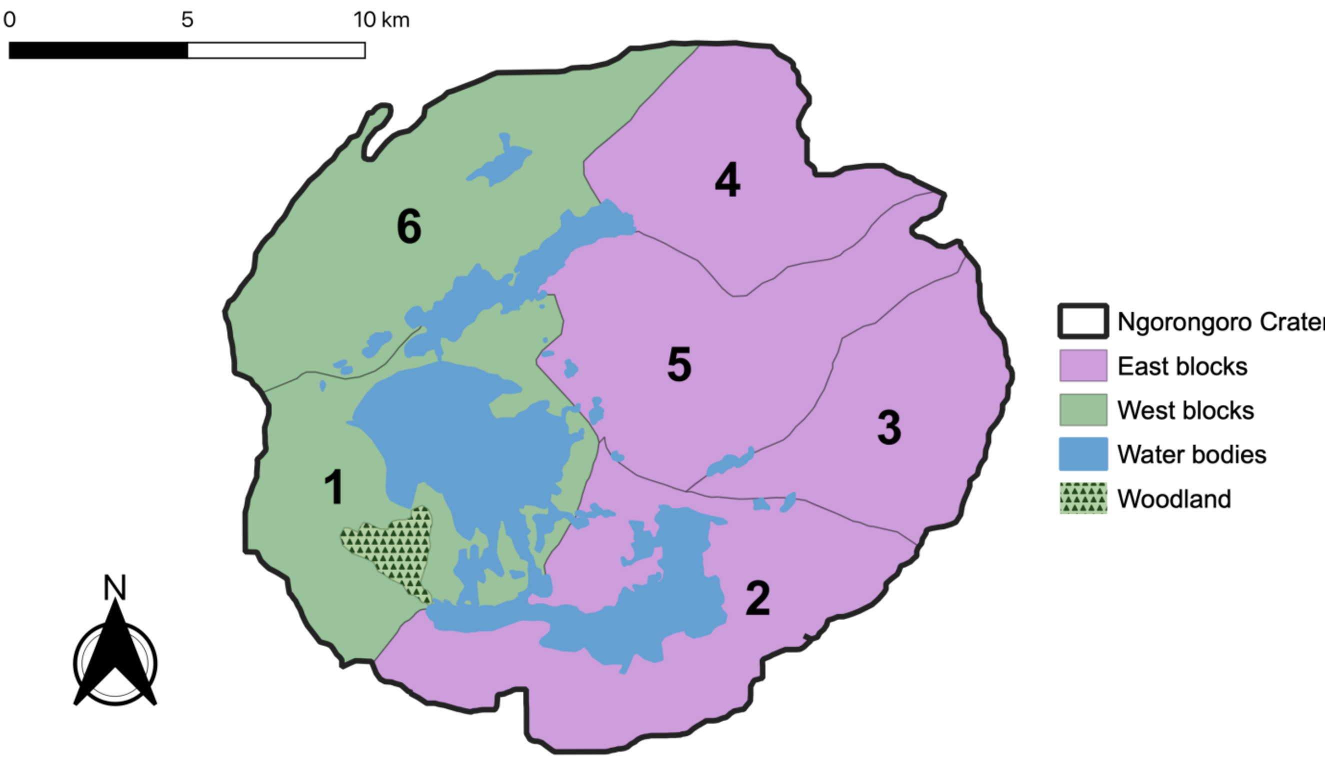

Figure S1: Ngorongoro Crater census blocks, delineated in the 1960s by the Ngorongoro Conservation Area Authority. Blocks are bounded by natural and anthropogenic barriers such as hills, roads, water bodies, woodlands. Block boundaries were slightly modified using georeferencing tools in QGIS (version 3.16.5-Hannover Long Term Release) such that roads between adjacent blocks were equally incorporated into the blocks rather than being treated as areas without prey because prey in navigable areas were included in census counts.

The difference in prey abundance between the east and west blocks increased between the periods (period 1: $mean_{east}$ = 2,632.8 ± 2,389.9, $mean_{west}$ = 3,660.9 ± 3,334.9; median of between-group differences = 179.3, CI95% = -631.2 - 1,599.0; Mann Whitney U test; n = 29 censuses; U = 2613.5, p = 0.02; period 2: $mean_{east}$ = 2,166.1 ± 1,448.1; $mean_{west}$ = 4,440.8 ± 2,360.7; median of between-group differences = 2,176.5, CI95% = 774.0 - 3,146.0; n = 9 censuses; U = 124, $p < 0.001$). These results indicate a biologically meaningful westward prey shift, justifying our decision to split clan territory calculations into two periods.

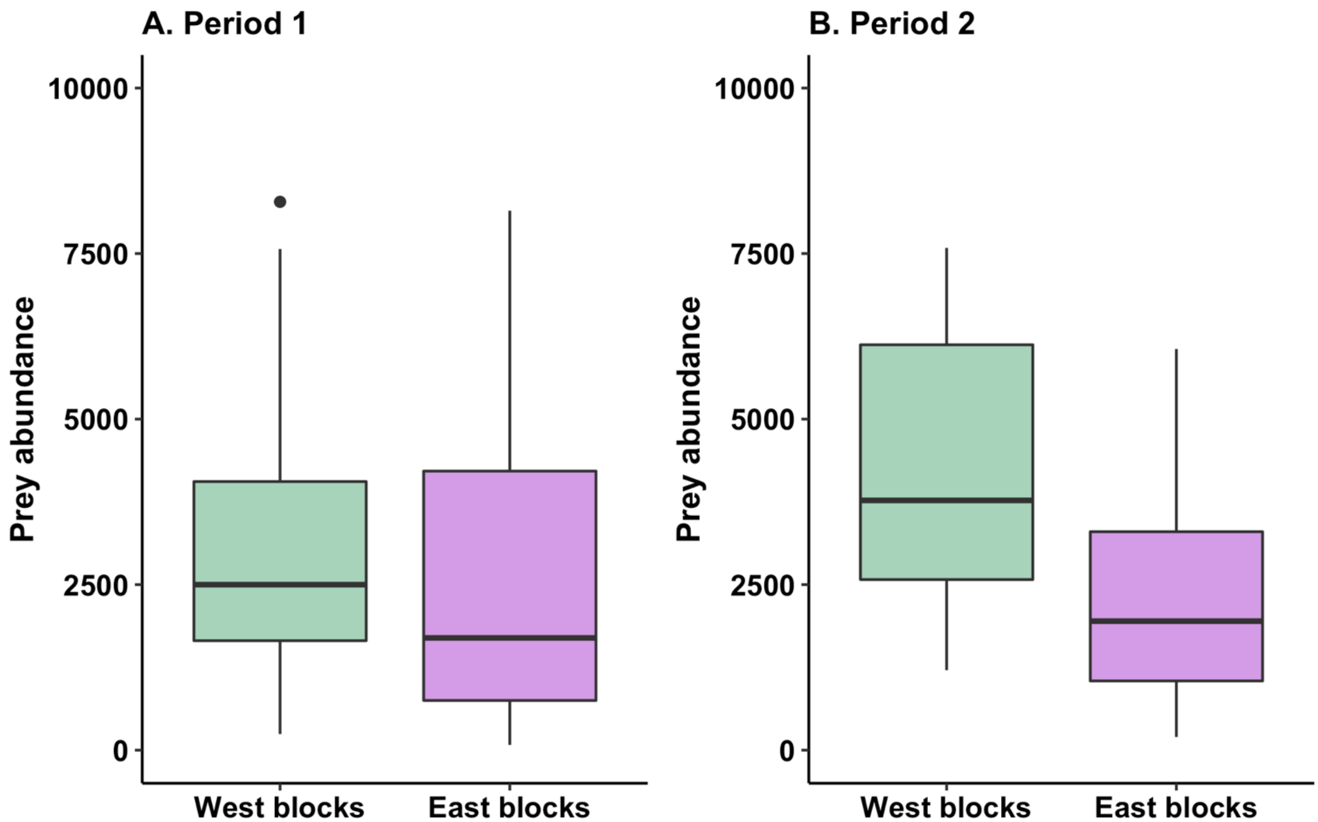

Figure S2: Box plots for Ngorongoro Crater wildlife census data showing disparities in spotted hyena prey abundance between east and west census blocks. **A.** Prey abundance in period 1 (1996-2011; east blocks = 116 counts; west blocks = 58 counts) **B.** Prey abundance in period 2 (2012-2019; east blocks = 36 counts; west blocks = 18 counts). The east blocks are comprised of blocks 2, 3, 4, and 5 while the west blocks are comprised of blocks 1 and 6 (Figure S1). Census data was collected on a bi-annual basis most years. Boxes indicate the interquartile range around the median (horizontal bar), vertical bars represent prey abundances that lie within 1.5 times the interquartile range. Dots represent data with a value greater than 1.5 times the interquartile range.

Table S1: Summary of MCP (minimum convex polygon) percentages used to define territories for spotted hyena clans. Territories were located in the Ngorongoro Crater, Tanzania and categorized into period 1 (1996-2011) and period 2 (2012-2019) due to major shifts in territory sizes and locations in 2012. Territories were based on the maximum MCP that still allowed for ≥90% fidelity to the focal clan in order to identify areas of near-exclusive access for the different clans. Fidelity was defined as the percentage of adult female sightings within the territory that were from adult females of the clan of interest.

Clan	**Period**	
	1	2
Airstrip	91%	98%
Engitati	84%	94%
Forest	95%	99%
Lemala	95%	96%
Munge	96%	99%
Ngoitokitok	61%	47%
Shamba	50%	99%
Triangle	95%	99%

B. Standardization procedure of fecal glucocorticoid metabolite measurements

Extracts from hyena fecal samples were assayed in two batches; one batch was run in July 2013 (Figure S3; n = 768 extracts, 23 plates) and another was run in July 2020 (n = 207 extracts, 18 plates). To ensure the comparability of the fGMC between the two batches, we applied a previously validated standardization method for fGMC (Davidian et al., 2015). The procedure involves three steps: (i) the re-assaying of a subset of extracts (n = 69 extracts) initially assayed in 2013, (ii) fitting a linear relationship between their 2013 and 2020 measurements, and (iii) applying the fitted equation to the fGMC measured for all other fecal extracts that were assayed in the 2013 batch to standardize fGMC to the performance and accuracy of the immunoassay for the 2020 batch. Of the 69 extracts that were re-assayed, 43 extracts had duplicated measurements that met the criteria for acceptance; i.e., they fell within the linear range of 1.5-20.0 pg/20µl and had the same dilution in 2013 and 2020 (Davidian et al. 2016). To obtain the standardization equation, we modeled the relationship between the initial fGMC measured in 2013 and re-measured fGMC in 2020. The model accounted well for the remeasured fGMC variation (Figure S4; adjusted $r^2 = 0.74$, n = 43).

Following established guidelines (Davidian et al. 2015), we deemed model predictions to be reliable if the coefficient of variation (CV_{fit}) between predicted fGMC and their corresponding remeasured fGMC did not exceed 20% ($CV_{fit} \leq 20\%$). We also considered a model to have acceptable predictive performance if more than 70% of samples had a $CV_{fit} \leq 20\%$. The cross-validation showed that 93% of samples (40/43) conformed to the criterion for acceptance of CV_{fit}, thereby demonstrating high predictive performance of the model equation. We then applied the model equation to standardize all measurements from 2013. In case a given sample had been assayed multiple times and had more than one acceptable result, we used the mean fGMC.

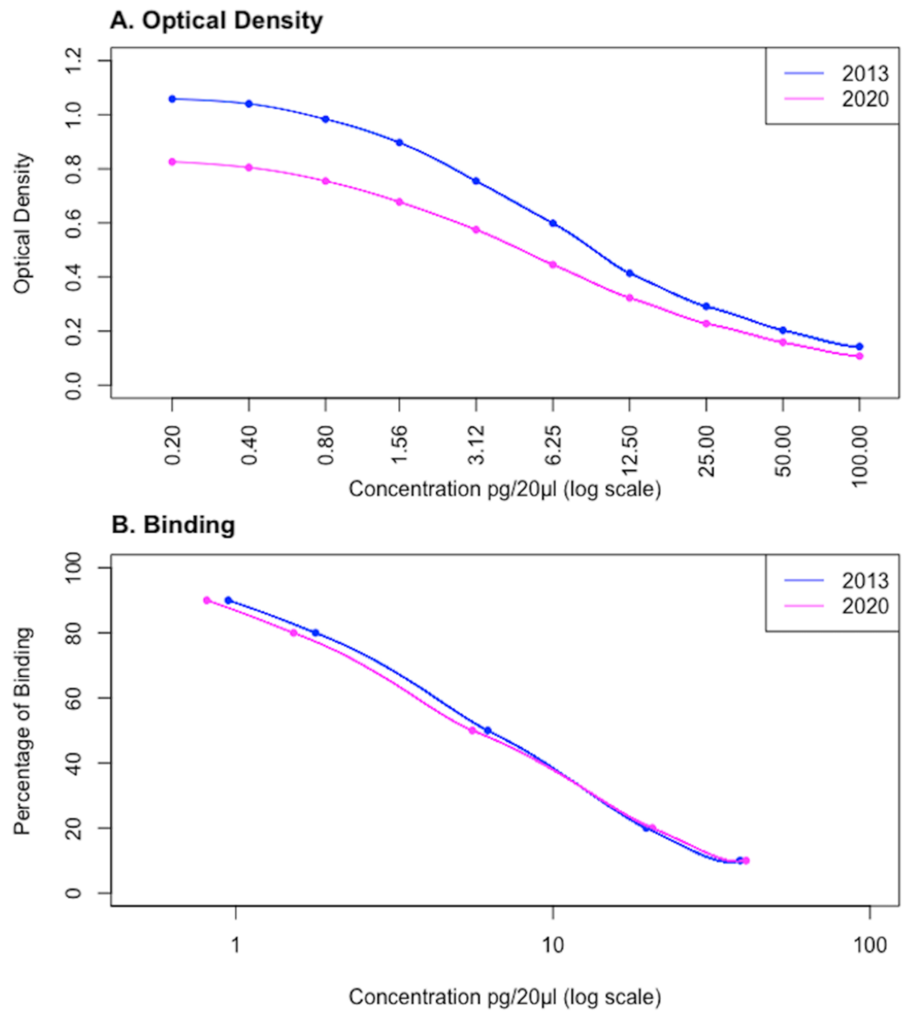

Figure S3: A. Cortisol standard calibration curves based on the mean results of batches of samples analyzed in 2013 (n = 23 assay plates) and 2020 (n = 19 assay plates) using an ELISA developed for cortisol-3-CMO. **B.** Relationship between the percentage of binding of the tracer and measured cortisol concentration in standards. Symbols in the binding curves correspond to the mean concentration in cortisol at 10, 20, 50, 80 and 90% of binding of the tracer.

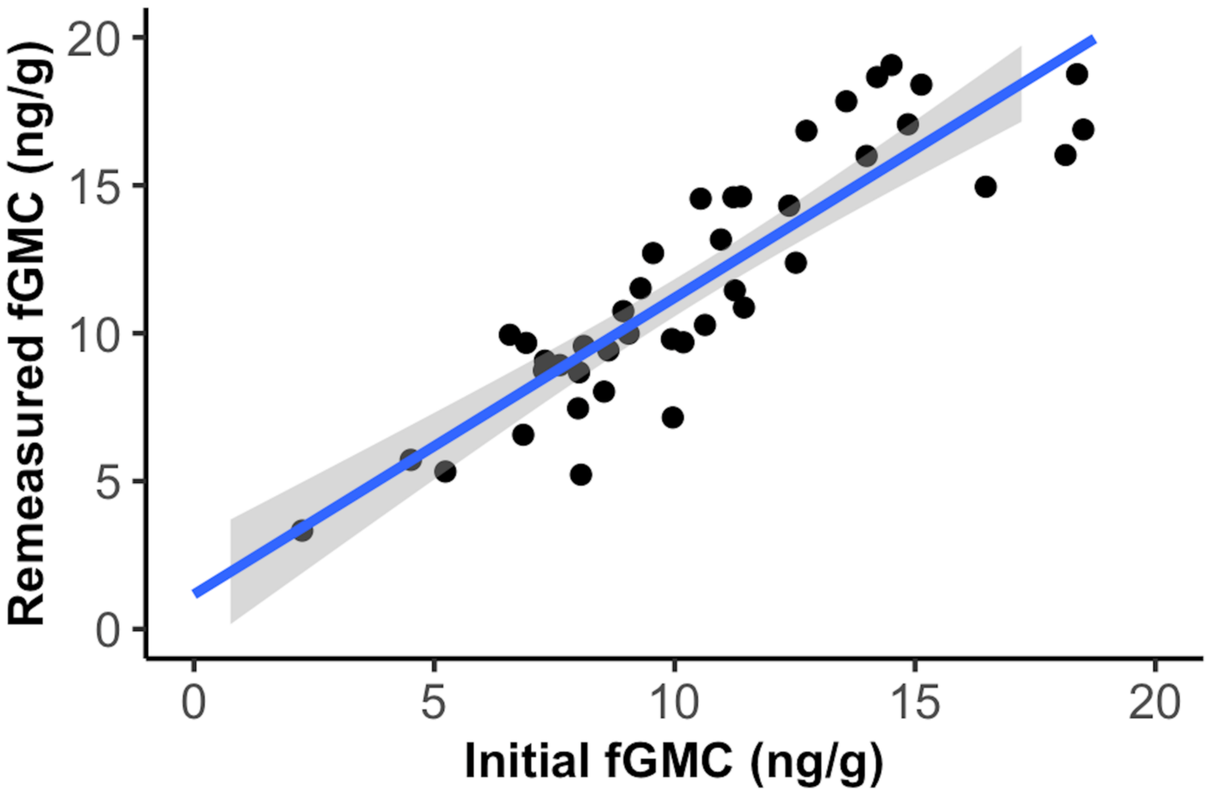

Figure S4: Relationship between initial (2013) and remeasured (2020) fecal glucocorticoid metabolite concentrations (fGMC) for a subset of 43 fecal samples. The blue line is the linear regression fitted to predict fGMC in the remeasured batch. The area shaded in gray represents the 95% confidence interval of the regression line ($fGMC_{remeasured} = 1.11 + 1.02*fGMC_{initial}$).

C. Additional assay controls and checks

EIA performance

To assess the performance of our enzyme immunoassay (EIA) in the two batches of measurements (2013 and 2020), we quantified the analytical sensitivity and quantitative resolution as in Davidian et al. (2015). We used the mean calibration curve for each batch of measurements to calculate the parameters for three standard values (1.56 ng/g; 6.25 ng/g; 25 ng/g; Table S2).

Table S2: EIA performance in terms of precision, stability of EIA accuracy, analytical sensitivity and quantitative resolution in 2013 and 2020. Stability of EIA accuracy and intra- and inter-assay precision were quantified through the coefficient of variation (CV) of repeated measurements of fecal pools with low ('low pool') and high ('high pool') metabolite concentrations. 'n' refers to the number of plates run within each batch of analyses. Though the $CV_{inter\text{-}assay}$ for the low pool of the 2020 batch was >20% due to stability issues in the laboratory, additional checks were conducted whereby low and medium concentration quality controls were run on later assays. Both the low and medium concentration quality controls performed well ($CV_{inter\text{-}assay}$ <20%), thereby confirming that the problem was isolated to the low pool and was not an assay issue.

		2013 (n = 23)	**2020 (n = 19)**
$CV_{intra\text{-}assay}$ (%)	Low pool	2	6
	High pool	1	4
$CV_{inter\text{-}assay}$ (%)	Low pool	15	22
	High pool	8	11
Analytical sensitivity	1.56 ng/g	0.091	0.066
	6.25 ng/g	0.030	0.020
	25 ng/g	0.004	0.003
Quantitative resolution	1.56 ng/g	0.15	0.12
	6.25 ng/g	0.16	0.64
	25 ng/g	1.99	1.43

Parallelism

We tested parallelism for both batches using an analysis of covariance (ANCOVA; Davidian et al., 2015). For the 2013 batch, ANCOVA validated parallelism for four fecal extracts (see Davidian et al., 2015). For the 2020 batch, ANCOVA also validated parallelism for all three extracts tested (n = 3; $F(1,5) = 0.21$, $p = 0.67$ for extract 'A'; $F(1,5) = 0.00$, $p = 0.99$ for extract 'B'; and $F(1,5) = 0.23$, $p = 0.65$ for extract 'C'). For the 2020 batch, parallelism was also tested on the extracts through serial dilutions and assessing the CV at the end for the different measurements. For all three extracts, the CV was below the threshold of 20%, confirming that there were no matrix effects (Davidian et al., 2015) on the measurements and that bias between measurements of metabolites and standards was constant throughout the range of applied dilutions.

Degradation of steroids in extracts and freeze-dried feces

Long-term storage of fecal samples and steroid metabolite extracts has previously been suggested to lead to temporal variation in their fGMC, e.g., due to evaporation of ethanol in extracts (Davidian et al., 2015; Kalbitzer & Heistermann, 2013). To assess if there was degradation of glucocorticoid metabolites in extracts and feces over the course of the seven years of storage at -80° C, we conducted a series of comparison of fGMC. The motivation behind this was to provide guidelines on best practices for long-term steroid storage.

First, to determine whether extracts 'aged' – i.e., whether the steroid they contain degraded – we compared the fGMC in extracts prepared and assayed in 2013 to the fGMC of the same extracts stored in our -80° C freezers and re-assayed in 2020 (n = 43). Second, to determine whether feces aged, we compared the fGMC in extracts from fecal extracts prepared in 2013 and assayed in 2020 (n = 27) to extracts from the same fecal samples prepared and assayed in 2020.

The fGMC of extracts assayed in 2013 (median = 10.20 ng/g) were significantly lower than the fGMC of the same stored extracts re-assayed in 2020 (Wilcoxon signed-rank test, median = 10.90 ng/g, V = 184, $p < 0.001$; median of between-group differences = -1.31 ng/g, CI95% = -0.39 - 2.00 ng/g; Figure S5A). In contrast, the fGMC from extracts prepared from fecal samples in 2013 and assayed in 2020 (median = 8.03 ng/g) were significantly higher than the fGMC from the same extracts prepared and assayed in 2020 (Wilcoxon signed-rank test, median = 8.12 ng/g, V = 298, $p = 0.008$; median of between-group differences = 0.64 ng/g, CI95% = 0.16 – 1.57 ng/g; Figure S5B). Though the results were statistically significant in both of these cases, effect sizes were small and therefore unlikely to be biologically meaningful (measurements in the different treatments differed by less than 2 ng/g). The mean CV between the 43 stored extract pairs was 12.7% (S.D.: 8.9%, range: 0.8% - 35.2%, CV <20% for 35/43 pairs) and for the 27 extract pairs from the same fecal samples, 10.5% (S.D.: 8.2%, range: 0.3% - 34.1%, CV <20% for 25/27 pairs). These results indicate that the fGMC of paired samples in both comparisons were similar across the years owing to the average CV being <20% and because >70% of the sample pairs in both comparisons had a CV of <20% (see Davidian et al. 2015 for details on criteria). We therefore conclude that fGMC degradation is not a major concern when extracts and fecal samples are stored for seven years.

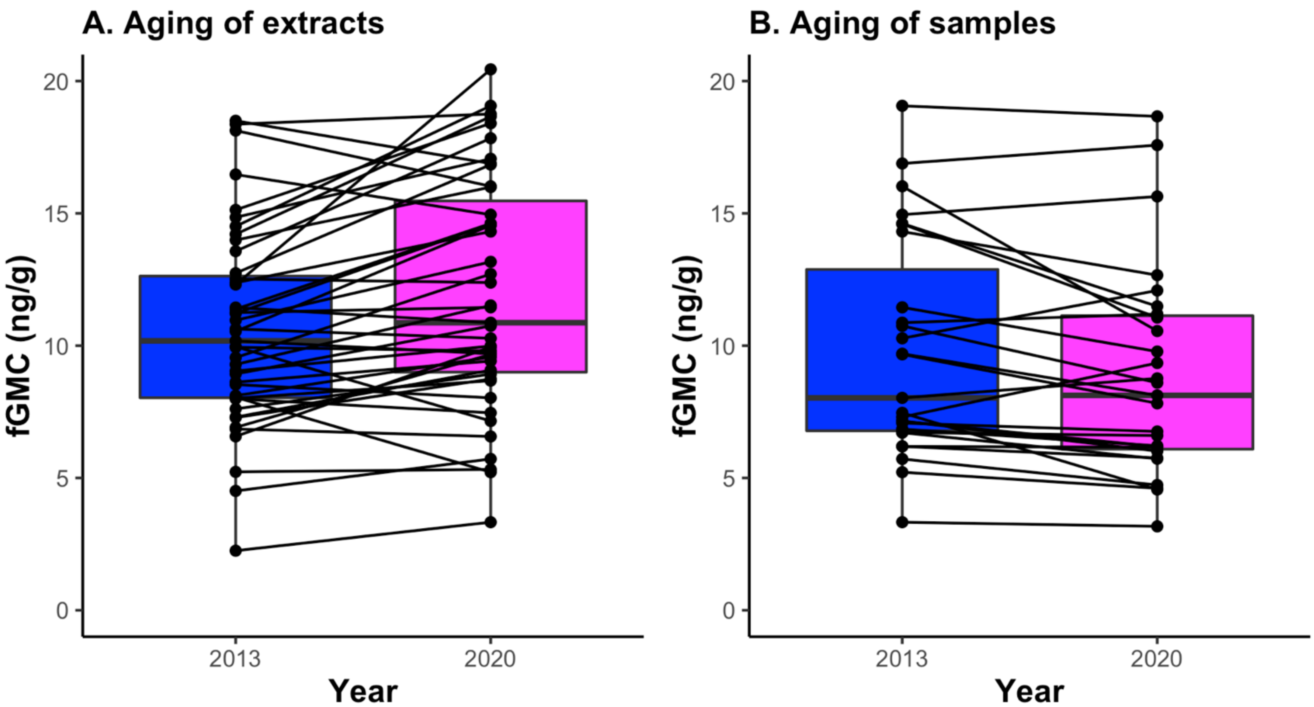

Figure S5: Changes in fecal glucocorticoid metabolite concentrations (fGMC) over the course of 7 years in extracts and feces. **A.** fGMC in extracts (n = 43) prepared and assayed in 2013, stored in -80° C freezers, and re-assayed in 2020. **B.** fGMC (n = 27) in extracts prepared 2013 and 2020 assayed in 2020. Data are raw concentrations, i.e., as assayed before accounting for the factor of dilution of the extract.

D. Interaction model results

Table S3: Effects of anthropogenic activity and ecological covariates on the number of juvenile recruits in spotted hyena clans. Covariates consist of anthropogenic activity (pastoralism), disease outbreaks, number of adult females, lion index, and prey per capita on the number of juvenile recruits produced by hyena clans in the Ngorongoro Crater, Tanzania. Also included is the interaction between anthropogenic activity and the other covariates. The intercept for the model corresponds to the exposed category of hyena clans (subject to pastoralism) and no disease outbreak, with the number of adult females, lion index, and prey per capita held at 0. Data in bold were deemed significant. Results are based on a negative binomial GLMM (p-values based on a likelihood ratio test using 999 parametric bootstrap replicates). Random variances were estimated for time- (n = 38 seasons) and clan-level (n = 8 clans) at 0.003 and 0.004, respectively. The coefficient for the temporal autocorrelation (AR1 structure) between consecutive seasons was estimated to 0.54. See Table 1 legend for details on column names.

	Estimate	**S.E.**	**% Change**	**L.R.**	***p***
Intercept	-0.98	0.90			
Unexposed	-0.39	0.94	32.0	3.49	0.63
Outbreak	-0.42	0.31	34.0	4.54	0.088
Adult females	**0.84**	**0.28**	**132.2**	**30.01**	**0.001**
Lion index	0.07	0.08	6.7	3.94	0.15
Prey per capita	0.00	0.00	0.0	3.14	0.21
Unexposed*Outbreak	0.02	0.33	30.9	0.00	0.97
Unexposed*Adult females	0.00	0.29	32.3	0.00	0.99
Unexposed*Lion index	0.00	0.08	32.2	0.00	0.98
Unexposed*Prey per capita	0.00	0.00	31.8	1.37	0.24

Table S4: Effects of anthropogenic activity and socio-ecological covariates on fGMC in hyenas. Covariates include anthropogenic activity (pastoralism), age, clan size, and proportional rank on the natural log of the fGMC of spotted hyenas in the Ngorongoro Crater, Tanzania. Also included is the interaction between anthropogenic activity and the other covariates. The intercept for the model corresponds to the exposed category of hyena clans (subject to pastoralism), with age, clan size, and standardized rank held at 0. Results are based on a gamma GLMM (p-values based on a likelihood ratio test using 999 para-metric bootstrap replicates). Random variances were estimated for time- (n = 41 seasons) and individual-level (n = 475 hyenas) at 0.003 and 0.005, respectively. The coefficient for the temporal autocorrelation (AR1 structure) between consecutive seasons was estimated to 0.55. See Table 1 legend for details on column names.

	Estimate	**S.E.**	**% Change**	**L.R.**	***p***
Intercept	1.18	0.08			
Unexposed	-0.02	0.08	-2.0	0.32	0.99
Age	**0.02**	**0.01**	**1.6**	**37.36**	**0.001**
Clan size	0.00	0.00	0.0	0.27	0.87
Rank	0.00	0.04	0.0	1.00	0.60
Unexposed*Age	0.00	0.01	-2.0	0.00	0.91
Unexposed*Clan size	0.00	0.00	-1.9	0.21	0.66
Unexposed*Rank	0.01	0.04	-0.6	0.12	0.74

E. Observed number of adult females

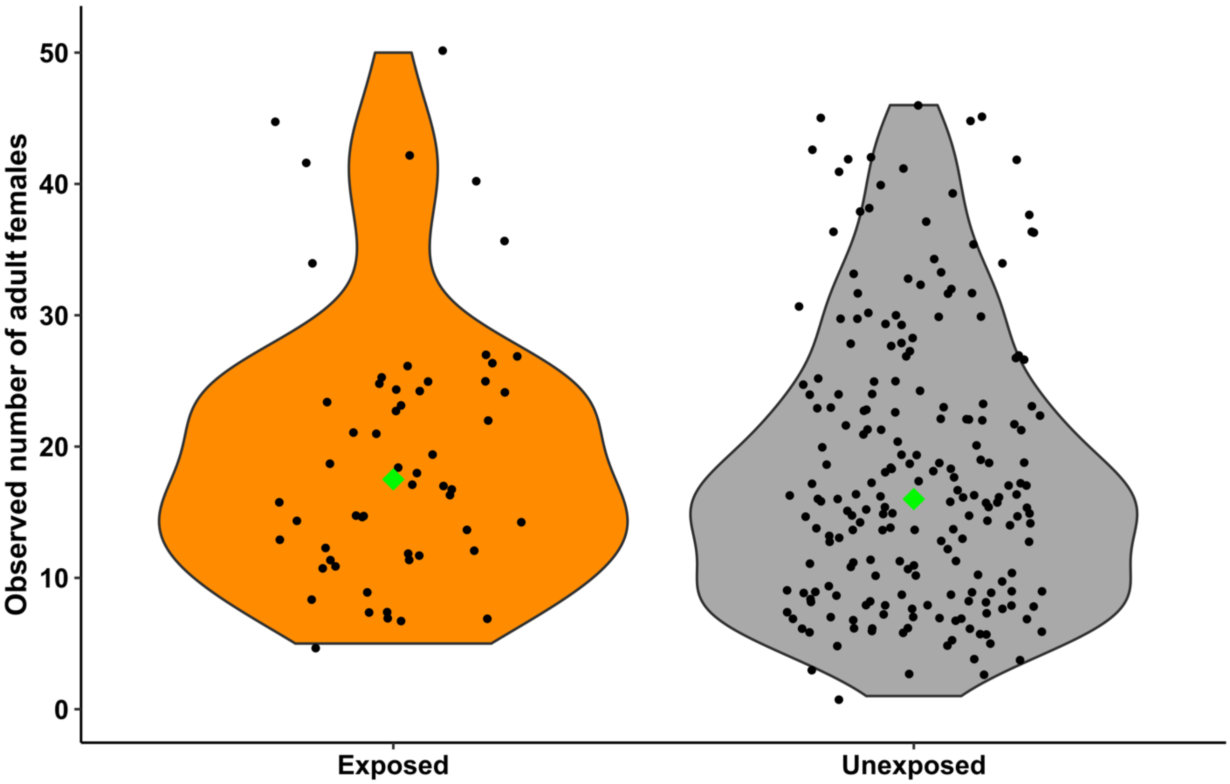

Figure S6: Observed number of adult females in hyena clans. The violin plot displays the distribution of data for the respective clan category (exposed or unexposed to pastoralism). Exposed clans (orange) were subject to pastoralism while unexposed clans (gray) were not. Black dots represent observed data after horizontal jittering was applied for ease of visualization. Green diamonds represent sample medians.

F. References

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Chapter 4

DNA metabarcoding provides answers to key conservation questions about spotted hyenas

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Manuscript in preparation.

Detailed contributions:

The conceptual framework and predictions of this study were developed by Arjun Dheer (AD) and Oliver Höner (OH). Demographic monitoring and the collection of samples was done by AD, Eve Davidian (ED), Philemon Naman (PN), OH, and Bettina Wachter. DNA extraction was done by AD, Renita Danabalan (RD), Antonia Pellizzone (AP), and Manon Quetstroey. Quantification of DNA concentration, PCR amplification and sequencing, quality control and analysis of sequences, and species assignments were conducted by AD, AP, and RD, under the supervision of Camila Mazzoni (CM). Data curation was handled by AD, PN, RD, and OH. Statistical analyses were conceptualized and conducted by AD and RD, under the guidance of CM and OH. The manuscript was primarily written by AD and RD, and edited by ED, CM, and OH.

DNA metabarcoding provides answers to key conservation questions about spotted hyenas

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Abstract

Using rigorous methods to assess the diets of large carnivores can answer questions of critical conservation and management importance in multi-use protected areas. In this study, we used DNA metabarcoding of 371 fecal samples collected over a 24-year period to determine the diet of spotted hyenas in the intensively-protected Ngorongoro Crater, Tanzania. We assessed whether the spotted hyenas regularly consumed the Critically Endangered black rhinoceros, a species of high conservation priority. We also investigated whether the hyenas foraged outside the Crater, which is surrounded by pastoralist areas, by determining if they consumed species that were only extant outside. In addition, we estimated their selection for 5 wildlife species based on long-term Crater census data. Finally, we quantified the effects of three key socio-demographic variables – age, rank, and sex – on the propensity of hyenas to consume domestic animals. In total, we detected 20 different species, comprising 434 total detections. We found 0 detections of black rhinoceros and 3 detections of Maasai giraffe, a species that did not inhabit the Crater. This suggests that the hyenas did not regularly consume black rhinoceros, but that they did leave the Crater to forage. Among wildlife species, they most strongly selected for blue wildebeest. Furthermore, we found a strong positive effect of age, but no detectable effect of rank or sex, on the propensity to consume domestic animals. Our study provides important insights for applied ecologists, local authorities, and stakeholders who seek to promote evidence-based large carnivore conservation. It also highlights the potential for DNA metabarcoding to answer important – and straightforward – wildlife conservation and management questions.

Keywords

Diet, DNA metabarcoding, black rhinoceros, domestic animals, Maasai giraffe, multi-use protected areas, spotted hyenas, Threatened species

1. Introduction

The effective management of multi-use protected areas (MUPA), where humans and wildlife cohabit, depends on gathering rigorous evidence to answer pressing conservation questions (Watson et al., 2016). Getting answers to such questions is especially urgent for Threatened wildlife species (Western, Russell, & Cuthill, 2009). Using such an evidence-based approach helps to balance the needs of priority wildlife species with those of local stakeholders, and the promotion of human-wildlife coexistence (Wevers et al., 2020).

However, there is currently a lack of evidence and conservation research conducted in protected areas worldwide (Coetzee, 2017). This has hamstrung evidence-based conservation and led to harmful management decisions that help neither people nor wildlife. For example, poorly-justified culling of rodents (*Rodentia* spp.) may have weakened multiple ecosystem services, reduced the food base for predatory birds and mammals, and caused habitat loss for other burrowing animals (Singleton et al., 2007). At a finer scale, management decisions may overlook individual-level tendencies in a population. For example, 'problem animals' may develop a predilection for consuming domestic animals, such as livestock. This behavior may be influenced by individual socio-demographic traits such as age, social rank, or sex (e.g., in brown bears (*Ursus arctos*): Morehouse et al., 2016). For instance, older age has been suggested to be positively associated with the killing of livestock or even humans by large carnivores (Reza, Feeroz, & Islam, 2002). This is because old individuals may be less capable of successfully hunting fleet-footed, powerful wild prey due to age-related disease and injury, and loss of dexterity, endurance, speed, and strength (Peterhans & Gnoske, 2001). In such cases, local communities may participate in indiscriminate retaliatory killing, or authorities may apply very broad conflict mitigation measures. This can have major negative impacts on populations and ecological communities, exacerbating the initial problem (Swan et al., 2017). There is accordingly an urgent need for using rigorous techniques to gather robust evidence to answer important conservation questions.

In this study, we assessed spotted hyena (*Crocuta crocuta;* henceforth 'hyena') diet to answer conservation questions in the intensively-protected Ngorongoro Crater, part of the Ngorongoro Conservation Area (NCA), a MUPA in Tanzania. Hyenas are apex predators and scavengers ranging across much of sub-Saharan Africa (Holekamp & Dloniak, 2010). The Crater hyena population has been the subject of a long-term study since 1996 (Höner, Davidian, & Szameitat, 2022). Past research has suggested that they exhibit considerable age-, rank-, and sex-related behavioral differences (Boydston et al., 2003; Yoshida, Van Meter, & Holekamp; 2016), though this has not yet been assessed in terms of diet. We thus assessed their diet to answer three conservation questions of high importance to the Ngorongoro Conservation Area Authority (NCAA) and of broad interest to applied ecologists and wildlife managers. First, we assessed if hyenas regularly consumed Critically Endangered black rhinoceros (hereafter 'rhino'; *Diceros bicornis*; Emslie, 2020) in the Crater, which is a key stronghold for the species. Second, we determined if hyenas left the Crater to forage in pastoralist areas outside, which would be proven by consumption of species only present outside the Crater (Estes, Atwood, & Estes, 2006). Third, we investigated how socio-demographic variables affect their propensity to consume domestic animals. To answer these questions, we used DNA metabarcoding of fecal samples.

DNA metabarcoding is an emerging, non-invasive technique to identify environmental DNA (eDNA) that is increasingly being used to assess the diets of wild carnivores (Havmøller et al., 2019; Morin et al., 2016). In this technique, scientists collect fecal samples from target species in the field. In the laboratory, eDNA is extracted from the sample, followed by high-throughput sequencing of taxonomically-informative markers to identify the DNA of consumed species (Alberdi et al., 2019). DNA metabarcoding poses three primary advantages over traditional morphological (e.g., hair) analyses of feces: it often detects consumed taxa otherwise missed, reduces representation bias associated with major differences in surface-area-to-volume ratios and hair densities across different species, and if necessary, can verify the identity of the putative consumer (Berry et al., 2017; Shehzad et al., 2015). Morphological approaches may also lead to misidentifications much more often than DNA metabarcoding does, especially between closely-related domestic and wild taxa (Monterroso et al., 2018). Though DNA metabarcoding cannot distinguish between hunting and scavenging (Toju & Baba, 2018), distinguishing the two behaviors was not the focus of our study. Thus, we chose to use DNA metabarcoding to (i) accurately identify consumed species, and subsequently, (ii) get answers to key conservation questions about the Crater hyena population.

We predicted that if the hyenas regularly consumed rhinos, then we would find at least one detection of rhino DNA. We also predicted that if the hyenas foraged outside the Crater, we would have at least one detection of DNA from species that were not extant in the Crater. Finally, we predicted that older age, lower social rank, and male sex would be positively associated with the propensity of hyenas to consume domestic animals.

2. Methods

2.1 Study area

Fieldwork took place in the Ngorongoro Crater (Figure 1), located in the Ngorongoro Conservation Area (NCA), Tanzania (03°12′36″S 35°27′36″E), part of the greater Serengeti ecosystem. The NCA is a MUPA established in 1959 and a United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site with a double mandate to protect the interests of wildlife and local human communities (Charnley, 2005). The NCA is inhabited by the Maasai tribe, a semi-nomadic, pastoralist ethnic group ranging from central Kenya to southern Tanzania (Fratkin, 2001). The Maasai resided in the Crater until 1974, when they were evicted and required to live in other parts of the NCA (Moehlman et al., 2020). They were still allowed to enter the Crater with livestock to conduct pastoralist activities during daytime, until this, too, was banned in 2016 (Melubo & Lovelock, 2019). All lab work occurred at the Leibniz Institute for Zoo and Wildlife Research and The Berlin Center for Genomics in Biodiversity Research, both located in Berlin, Germany (52°31'12"N 13°24'17"E).

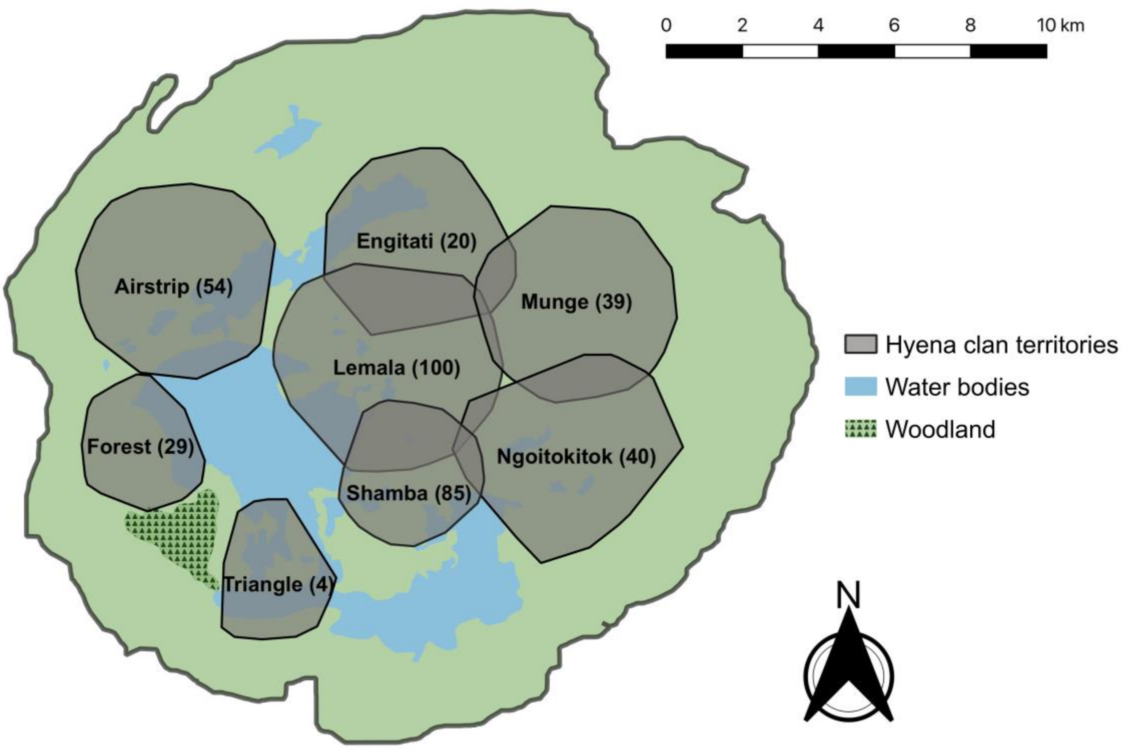

Figure 1: Hyena clan territories in the Ngorongoro Crater. Territory boundaries are based on 85% minimum convex polygons of adult female hyena sightings from 1996-

2019 for each clan. MCP of 85% were chosen to accurately represent the locations and sizes of clan territories across the study period. Territories are labeled with corresponding clan names. Numbers in parentheses indicate the number of samples we analyzed from the corresponding clan.

Throughout our study period, the Ngorongoro Crater was exceptionally rich in wild ungulates (Moehlman et al., 2020; Wachter et al., 2002). Additionally, over the course of our study, the cattle (*Bos taurus*) population more than doubled from under 120,000 to over 240,000 and the human population from under 43,000 to over 100,000 in surrounding parts of the NCA (Manzano & Yamat, 2018). Meanwhile, the donkey (*Equus asinus*), goat (*Capra hircus*), and sheep (*Ovis aries*) populations also greatly increased to over 20,000, 220,000, and 340,000, respectively (National Bureau of Statistics Tanzania, 2017). Other domestic animals in the NCA included cats (*Felis catus*), chickens (*Gallus gallus*), dogs (*Canis familiaris*), dromedary camels (*Camelus dromedarius*), and pigs (*Sus domesticus*).

2.2 Data collection

Collection of field data occurred between April 1996 and December 2019, on a near-daily basis, between 06:00 and 19:00. We recognized individuals based on their pelage patterns, ear notches, scars, and other traits. Ages were estimated based on pelage, body size, behavior, and locomotion, with an accuracy of ±7 days (Pournelle, 1965). Sexes were identified through observation of external genitalia (Frank, Glickman, & Powch, 1990). We collected fecal samples opportunistically, immediately after defecation by identified individuals. Following collection, feces were mechanically mixed, subsampled, stored in liquid nitrogen, and then transported to the laboratory in Berlin, Germany, on dry ice, where they were stored at -80°C until processed for extraction and analyses. We conducted lab work between May 2019 and March 2021.

2.3 Molecular methods and socio-demographic representation

2.3.1 DNA extraction

We extracted DNA from 505 fecal samples using a Stool DNA Kit (Roboklon GmBH, Berlin, Germany), following manufacturer instructions, with minor adjustments. We placed at least 200mg of feces into individual bead tubes from the kit and then homogenized the sample (Tissue Lyser II, Qiagen, Germany) 2 times for 20 seconds. We used the entire lysate for the remaining extraction procedure. We eluted samples in a final volume of 70µl and measured the concentration of extracted DNA using a Qubit 3.0 Fluorometer (Thermo Fisher Scientific, Germany). We then stored samples in a -20°C freezer until sequencing took place.

2.3.2 Sequencing summary

Out of the 505 fecal samples, we retained results from 371 (73.5%) for our analyses. Of the 124 we removed, 31 had low total read counts (<1,000; Johnson, Lewandowski, & Merkes, 2021). Another 70 had, in addition to low read counts, DNA concentrations too low (n = 63; <50 ng/µl) or high (n = 7; >600 ng/µl) to be reliably sequenced (Koetsier & Cantor, 2019). We could not identify a clear reason as to why these samples did not work; possibly, inhibitors were present in these samples, preventing amplification of the desired fragment (De Barba et al., 2013). The remaining samples that we removed (n = 23) were either duplicates derived from the same stool (i.e., samples collected from the same 'defecation event'), or definite cases of contamination. For example, we had one sample with a total read count of ≥1,000, and most of its reads were of red fox (*Vulpes vulpes*), which are not extant in the NCA, let alone sub-Saharan Africa (Hoffman & Sillero-Zubiri, 2016). Thus, we excluded the results from this sample. Of the 371 samples we retained, 64 had read counts between 1,000-2,000, 95 between 2,000-3,000, and 212 >3,000. We will provide summary read count plots in a future supplementary material.

2.3.3 Representation of socio-demographic variables

We collected the 371 samples from 255 individual hyenas, all of which were ≥1 year old on the date of collection. The hyenas represented all eight Crater clans (Figure 1). 234 samples (63.1%) were from males and the remaining 137 from females. The collection year of samples ranged from 1996 (n = 9) to 2019 (n = 39), with a peak in 2018 (n = 78; Figure S1).

2.3.4 PCR amplification and sequencing

Because DNA in fecal samples can be heavily degraded, we used a 108-base pair (bp) fragment within the 12S rRNA gene (Riaz et al., 2011) with a two-step metabarcoding protocol. Briefly, vertebrate DNA was first amplified with primers containing Illumina adapters and a blocking primer specifically designed to inhibit the amplification of host DNA (i.e., hyena DNA; 5´-AGATACCCCACTATGCCTAGCCCTAAACTCAGATAGATAATT-Spacer_C3- 3´). Depending on the DNA concentration, we used either 5µl or 200ng of DNA in a 20 µl PCR containing 1X Herculase buffer, 0.2nM of both dNTPs and forward and reverse primer, 10nM of blocking primer, 4nM of Mg^{2+}, and 1.25U of Herculase II polymerase. Thermocycling conditions included an initial denaturation at 95°C for 5 minutes, followed by 35 cycles of 94°C for 30 seconds, 60°C for 30 seconds and extension at 72°C for 1 minute and ended with a 10-minute final elongation step at 72°C. We cleaned the PCR products using CLEAN NGS magnetic beads (GCBiotech, Netherlands) in a 0.8:1 ratio of beads to product and washed them twice, using 80% EOTH. We re-suspended products in 25µl of 0.1X T.E. buffer, and then recovered 24µl for the second PCR step. In order to de-replicate the individual samples post-sequencing, we PCR-ligated each sample with a unique combination of P7 and P5 indices, containing the sequencing primer and part of the flow cell adapter. As such, we added 10 µl of cleaned PCR product to a 15 µl mixture containing 1X Herculase buffer, 0.1nM dNTPs, 4% DMSO, 0.21U of Herculase II Polymerase and 0.25nM of both P7 and P5 indices. Thermocycling conditions included an initial denaturation at 95°C for 5 minutes, followed by 12 cycles of 94°C for 30 seconds, 52°C for 30 seconds, extension at 72°C for 1 minute, and ended with a 10-minute final elongation step at 72°C. We cleaned the now-indexed samples using the method described after the first PCR. Quantification of cleaned libraries were measured using a Quant-iT™ Picogreen™ dsDNA High Sensitivity Assay Kit (Thermo Fisher Scientific, Germany). Based on the concentration, we pooled samples equi-mass with 15ng of DNA. We cleaned the pool twice to remove any remaining primer dimers or sequencing products that were less than 100 bp, using the steps outlined above. We recovered a total of 20µl following the final elution. We checked libraries for a single fragment size of 320 bp using an Agilent Tapestation (Applied Biosystems, Germany) and quantified in replicate using a Qubit 3.0 Fluorometer (Thermo Fisher Scientific, Germany). We carried out sequencing on a MiSeq, v3 600 Cycles Reagent Kit (Illumina, U.S.A.).

2.3.3 Quality control and analysis of sequences

We assessed all reads for quality using ‘FASTQC’ (Babraham Bioinformatics, England) and ‘MultiQC’ software (Ewels et al., 2016). After analyzing both the number of reads generated per sample and the MultiQC output, we only retained samples with a total read count of ≥1,000 (Clarke et al., 2020). We assembled read 1 and read 2 using Paired End reAd mergeR (PEAR, HITS, Heidelberg, Germany) and trimmed them, keeping those with quality ≥18 by defining it with parameter: *-q 18*. We removed primers using cutadapt: *-g forwardprimer…reverseprimer*, specifying that adapters are linked and requiring both to be removed (Martin, 2011). We removed chimeras using abundance rather than a reference with *Uchime_denovo* with the ‘Vsearch’ programme (Rognes et al, 2016) after de-replication. Following the removal of chimeras, we re-replicated samples and appended sample names into the header of the sequence using *Obiannotate –sample S:sample_name*, within the ‘OBItools’ programme (Boyer et al., 2014). We de-replicated sequences again using *Obiuniq – m sample*, as the output contained the number of reads for each unique sequence cluster. Based on the read counts in the *Obiuniq* output, we only retained sequences with read counts of ≥5% of the total count within the sample (‘countinreads.py’ script in future supplementary material). Finally, we allocated species assignments using a BLASTn search on Genbank, which contains a reference library of over 450,000 formally described species (Sayers et al., 2020), including all terrestrial mammals known to be extant in the NCA. We assumed each individual detection of a given species’ DNA in a sample represented one ‘meal’, i.e., one case of the hyena eating an animal of that species (Davidson et al., 2019; McLennan et al., 2022).

2.4 Age, rank, sex, and species categories

We attributed an age, rank, and sex to each sample based on the defecating hyena’s age in years, its ordinal rank on the day of sample collection, and its (constant) sex. We determined ordinal ranks based on the history of recorded agonistic interactions and our knowledge of rank inheritance and social queuing (for details, see Davidian et al., 2021). We converted the ordinal rank (*OrdRanki*) of an individual (*i*) into a proportional rank (*PropRanki*) bounded between -1 (bottom rank) and 1 (top rank), accounting for clan size *N*, using the following formula:

$$PropRank_i = \frac{N - OrdRank_i}{\frac{N-1}{2}} - 1$$

We estimated the effects of hyena age (in years: numeric and continuous), rank (proportional: between -1 and 1), and sex (categorical: female or male) on the propensity of hyenas to consume domestic animals using a generalized linear mixed-effects model (GLMM) with a binomial distribution using package 'lme4' (Bates et al., 2015). We used the binomial distribution because the response variable was categorical, with two levels: 'domestic' or 'wild', depending on whether the given detection was of a domestic or wild animal species. We included a random effect for the ID of the fecal sample, given that some samples had more than one species detected.

We computed predictions and associated 95% confidence intervals from the GLMM for any significant independent variable(s) using the function 'ggemmeans' from package 'ggeffects' (Lüdecke, 2018). For ease of interpretation, we calculated the percent change in the absolute value of the probability of domestic animal consumption resulting from a one-unit change in the value of the focal independent variable compared to its reference, calculated as [exp(coefficient)−1]*100.

2.5 Species selection

We used data from biannual, transect-based Crater censuses (n = 43) to estimate the composition and size of the typically available food base for the hyena population over the course of our study period.

Following this, we used Manly's standardized selection ratio *B* (Manly, McDonald, & Thomas, 1993) to determine selection for the different species using package 'adehabitatHS' (Calenge, 2006). The ratio *B* provides an estimate of selection for a given resource (i.e., the consumed species) relative to selection for all other resources, based on the proportional availability of each resource within the entire community. The value of *B* is the probability that a randomly chosen detection of any species will belong to a given species, if all species are equally frequent in the original population (Manly, McDonald, & Thomas, 1993). Thus, the ratio can range from 0 (minimum selection) to 1 (maximum selection). We also used a chi-square test with Bonferroni-corrected p-values to determine if the proportional consumption of each species was significantly different than its corresponding proportional availability.

In order to ensure our estimates of *B* were rigorous, we only included species for which there were reliable census data and for which there were at least 10 detections.

2.6 Statistical analyses

We conducted all statistical analyses in R software 4.2.0 (R Core Team, 2022). Data are presented as means ± S.D., unless stated otherwise. The threshold for statistical significance was set to $\alpha = 0.05$.

2.7 Verification of results

To verify our ability to distinguish between the DNA of cattle (the most important livestock species to the Maasai community; Goldman, 2011) and the closely-related African buffalo (*Syncerus caffer*; henceforth 'buffalo'), we conducted a feeding experiment with a hyena housed at Tierpark Berlin, a zoo in Berlin, Germany, in 2019. On a designated morning, the hyena keeper fed the hyenas exclusively cattle meat (beef). The next morning, based on the speed of the hyena digestive process (4-48 hours; authors' observation; Goymann et al., 2019), the keeper collected and passed a fecal sample from the hyena on to us. Following analysis, the only species detected from the sample was cattle.

In addition, we were able to retroactively verify the results of 3 samples based on direct field observations. First, we observed a hyena eating wildebeest on 1998-07-06. On 1998-07-07, we collected a fecal sample from the same hyena, which had ≥5% of its total reads from wildebeest. Second, we observed a hyena eating buffalo on 2012-11-28. On 2012-11-29, we collected a fecal sample from the same hyena. According to our analyses, the sample contained ≥5% of its total reads from buffalo. It however also contained ≥5% of its total reads from wildebeest. Though we did not see this hyena eating wildebeest on 2012-11-28, it likely did so at a time when we were not with it (e.g., at night, given that we were restricted to daytime observations). Finally, on 2018-03-19, we collected a sample from a hyena that we saw eating wildebeest carcass 6 hours prior to sample collection. Following analysis, the only species detected was wildebeest.

3. Results

3.1 Detections according to species

We detected 20 different animal species in the 371 samples (Figure 2). The total number of detections – inclusive of all species – was 434. The majority (n = 312; 84.1%) of samples only had one species, followed by those with two (n = 55) and three (n = 4).

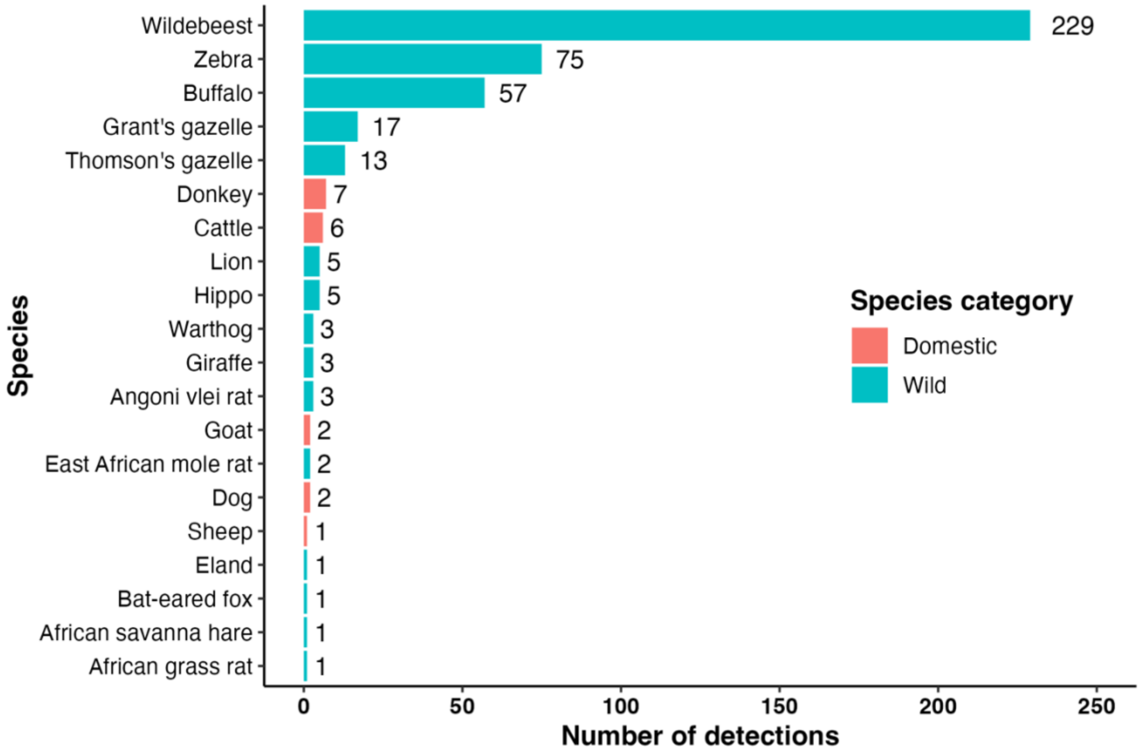

Figure 2: Total number of detections of DNA of different species in hyena feces from the Ngorongoro Crater. There were 434 total detections across 371 samples. Each detection represents one case of DNA of the given species being detected. Detections were classified as 'domestic' (domestic animal species) or 'wild' (wild animal species) and are color-coded accordingly.

There were 0 detections of rhino and 3 detections of Maasai giraffe (*Giraffa camelopardalis tippelskirchi*; henceforth 'giraffe'; a species only extant outside the Crater). We also detected 5 domestic animal species: cattle, dog, donkey, goat, and sheep, comprising 18 detections (4.2% of total). Among wild animals, blue wildebeest (*Connochaetes taurinus*; henceforth 'wildebeest') was by far the most commonly-detected species, followed by plains zebra (*Equus quagga*; henceforth 'zebra') and buffalo.

3.2 Detections according to socio-demographic variables and species categories

The hyena age attributed to domestic animal detections (mean = 9.08 ± 4.16 years, n = 18) was significantly greater than those attributed to wild animal detections (6.19 ± 3.04 years, n = 416; two-sample permutation test; Z = 3.82, $p < 0.001$; Figure 3A). In contrast, there was no significant difference in the proportional rank of hyenas attributed to domestic animal detections (-0.39 ± 0.62, n = 18) and that of hyenas attributed to wild animal detections (-0.23 ± 0.63, n = 416; Z = -1.06, p = 0.29; Figure 3B).

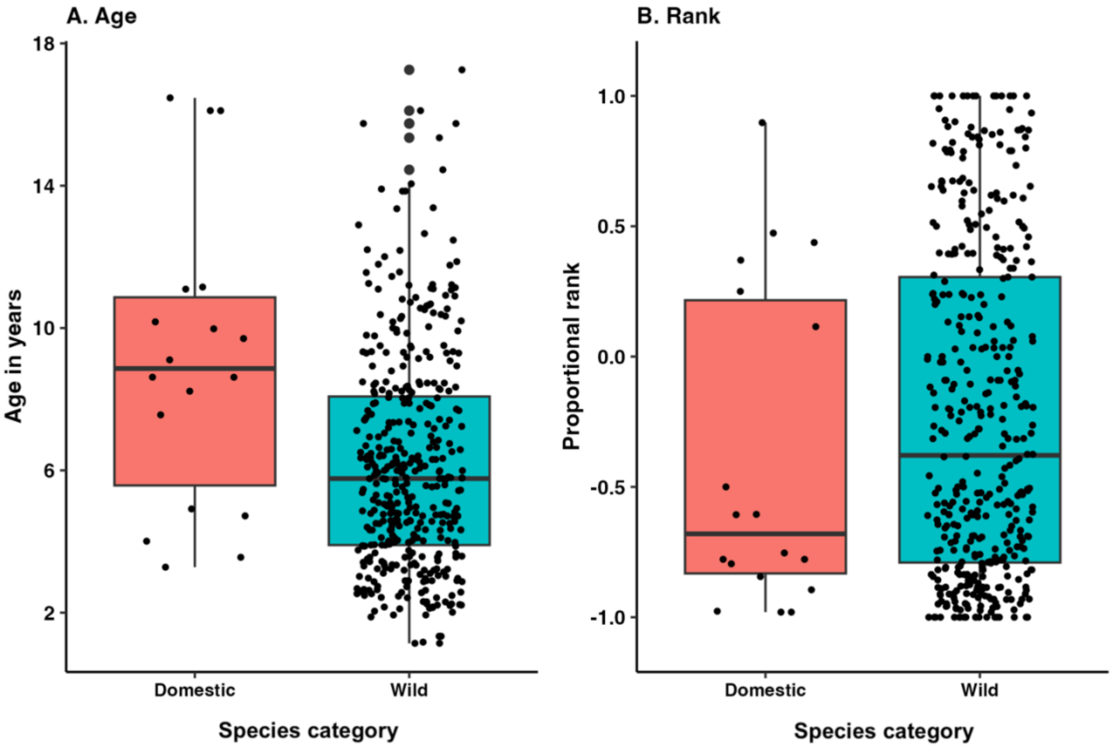

Figure 3: Relationship between consumption of domestic animals and socio-demographic variables in hyenas. A. Age and **B. Rank**. Each box plot displays the distribution of detections within the respective category. Species were categorized as domestic (domestic animals) or wild (wild animals). The age and rank attributed to a given sample were based on the defecating hyena's age in years and proportional rank on the date of sample collection. Boxes indicate the interquartile range around the median (horizontal bar), vertical bars represent data that lie within 1.5 times the interquartile range. Large black dots represent data with a value greater than 1.5 times the interquartile range. Small black dots represent observed data after horizontal jittering was applied for ease of visualization.

The majority of all detections (n = 273; 62.9% of all detections; Figure 5) were from males. Similarly, the majority of both domestic (n = 13; 72.2%) and wild (n = 260; 62.5%) animal detections also came from males.

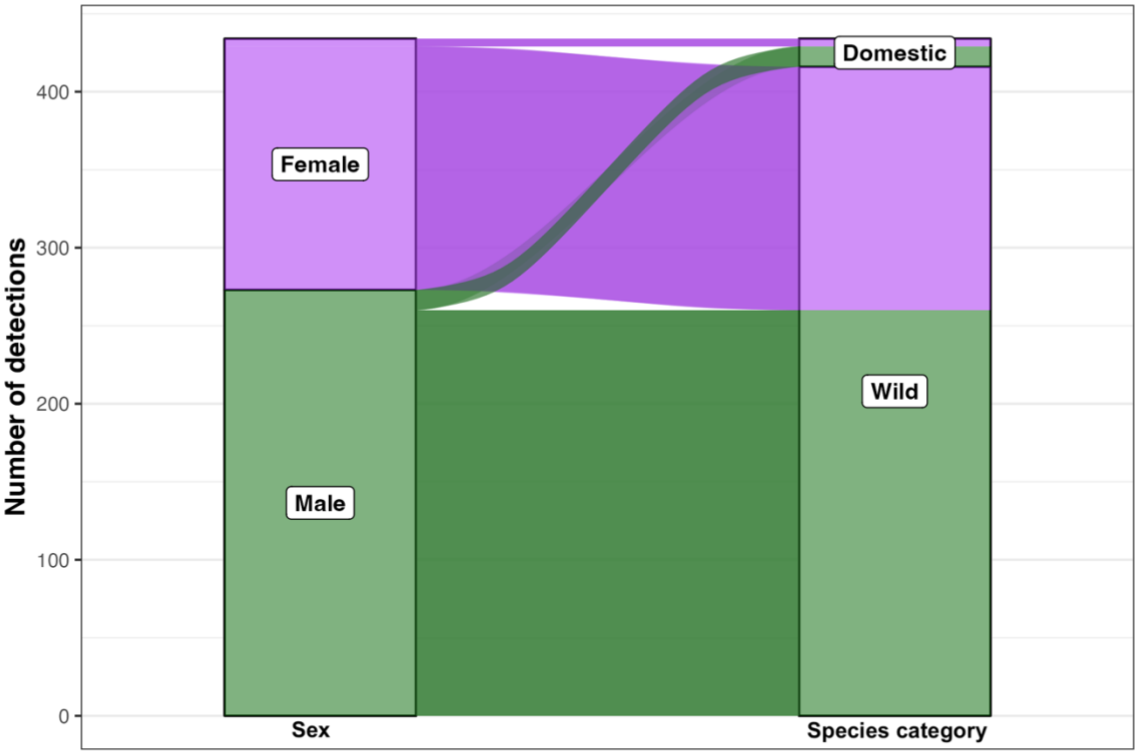

Figure 4: Alluvial plot showing distribution of detections based on hyena sex and species category. A total of 434 detections of domestic and wild animal species from 371 fecal samples are represented in the plot. Purple and green bands represent detections from female and male hyenas, respectively. The thickness of bands corresponds to the sample size. The size of the blocks for each category in the axes 'Sex' and 'Species category' also correspond to sample size.

3.2.1 Model results

There was a significant effect of age (positive), but not rank or sex, on the predicted probability of domestic animal consumption (Table 1). A one-year increase in a hyena's age led to a predicted 26.8% increase in the probability of domestic animal consumption (Figure 6).

Table 2: Effects of socio-demographic variables on the propensity of hyenas to consume domestic animals. Covariates consist of age, rank, and sex. The intercept for the model corresponds to the domestic species category and the female sex, with age and rank held at their means. The column "S.E." provides standard errors on parameter estimates. The column "% Change" gives the percent change in the absolute value of the response variable resulting from a one-unit change in the value of the focal predictor

compared to its reference. The columns "Z" and "*p*" give, respectively, the Z- and p-values associated with the likelihood ratio test. Data in bold were deemed significant. Results are based on a binomial GLMM. Random variance was estimated for sample ID (n = 371 samples) at 0.74.

	Estimate	**S.E.**	**% Change**	**Z**	***p***
Intercept	-5.35	0.87			
Age	**0.24**	**0.07**	**26.8**	**3.29**	**0.001**
Rank	-0.07	0.63	-6.6	-0.11	0.91
SexMale	0.55	0.83	73.2	0.66	0.51

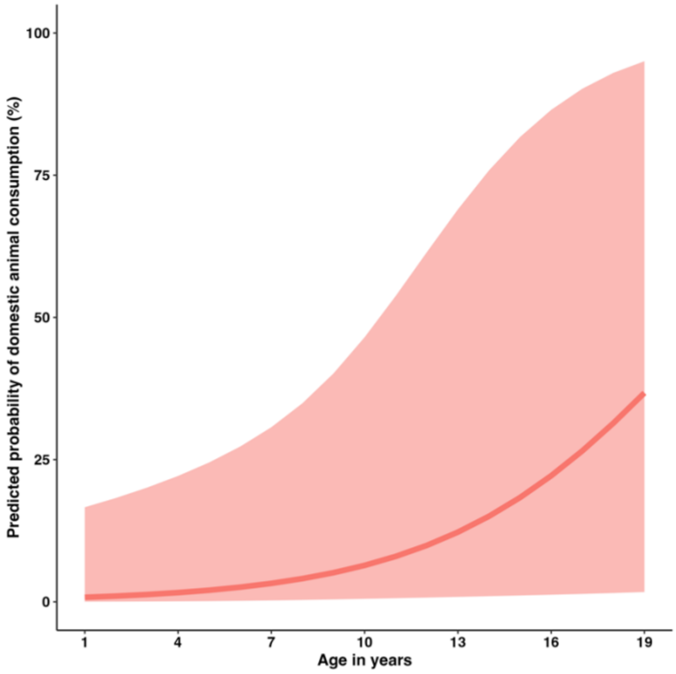

Figure 5: Effect of hyena age on predicted probability of consuming domestic animals. Predicted probability was calculated based on changes in a hyena's age (in years), averaged over the proportions of the categories of other factors (i.e., generalized to the sample population), and of the inferred random effect of sample ID.

3.3 Selection according to species

Wildebeest was selected for the most strongly, followed by Grant's gazelle (*Nanger granti*), buffalo, zebra, and then Thomson's gazelle (*Eudorcas thomsonii*; Table 1).

Table 1: Selection for wildlife species by spotted hyenas in the Ngorongoro Crater. Abundances were based on transect surveys (n = 43) conducted within designated census blocks from 1996-2019 by the Ngorongoro Conservation Area Authority, usually bi-annually. Presented here are the 5 species included in the selection estimates in this study, based on the reliability of their abundance estimates and the fact that each had at least 10 detections. Column "***B***" provides Manly's standardized selection ratio for the given species, with higher values indicating greater selection for the given species. Columns "χ^2" and "***p***" provide the chi-square test statistic and Bonferroni-corrected p-value, respectively, for the proportional consumption and availability of each species. Column "**Sign**" shows whether the proportional consumption was significantly greater than expected (+), less than expected (-), or as expected (0). Data in bold were deemed statistically significant.

Species	Abundance ± S.D.	*B*	χ^2	*p*	Sign
Wildebeest	**8,218.8 ± 2,924.4**	**0.30**	**25.75**	**<0.001**	**+**
Grant's gazelle	**833.7 ± 396.4**	**0.22**	**5.58**	**0.018**	**+**
Buffalo	3,176.8 ± 1,540.1	0.19	3.16	0.075	0
Zebra	4,274.1 ± 1,331.1	0.19	0.09	0.76	0
Thomson's gazelle	**1,392.4 ± 632.0**	**0.10**	**24.15**	**<0.001**	**-**

4. Discussion

In this study, we used DNA metabarcoding to assess the diet of hyena clans in the Ngorongoro Crater, Tanzania, over a 24-year period. We sought to understand whether the hyenas regularly consumed rhinos and whether they left the Crater to forage in surrounding areas. We also assessed the effects of socio-demographic variables on the likelihood of hyenas to consume domestic animals. We found 0 detections of rhino DNA and 3 detections of giraffe DNA, proving that the hyenas at least sometimes left the Crater to forage. Overall, their diet was dominated by wild animals, with few detections of domestic animal DNA. Additionally, older age was associated with increased likelihood of consuming domestic animals. Below, we provide possible explanations for and interpretations of our results in the context of evidence-based large carnivore conservation.

We found 0 detections of rhino DNA, which suggests that the Crater hyenas did not regularly consume rhinos. This indicates that they likely do not pose a credible threat to the Crater rhino population, which underscores their ability to coexist and the likelihood of the rhino population's persistence in the Crater. The potential effect of hyena predation on rhinos has been raised as a major conservation issue in East Africa, but such concerns have lacked robust evidence (Davidson et al., 2019; Sillero-Zubiri & Gotelli, 1991). Our results may assuage such concerns. While we acknowledge the possibility that hyenas do sometimes prey upon or scavenge rhinos, our study – based on 371 samples collected over a 24-year period – indicates that it is very unlikely to occur regularly, at least in the Ngorongoro Crater, which is a stronghold for the species. This lack of predation may be because rhinos are massive, formidable prey for hyenas (Owen-Smith & Mills, 2008). We consider this result a positive sign of the rhino population's continued persistence, due to ongoing conservation efforts geared towards the species by the NCAA and an evident lack of predation pressure by hyenas.

We also found 3 detections of giraffe and 18 of domestic animals. While the number of detections of both were low, they prove that hyenas at least occasionally entered areas outside the Crater. This has implications for conservation management in the Crater and surrounding areas. First, it affirms that the Crater hyena population is connected to populations outside, which is a positive indication of landscape connectivity and gene flow for this keystone, apex predator. Second, it also highlights that Crater hyenas may occasionally conduct livestock depredation and/or beneficial scavenging of dead livestock. Though livestock entered the Crater through 2016, they only did so in the daytime and were very well-protected by Maasai pastoralists (Dheer et al., 2022). Thus, Crater hyenas likely consumed domestic animals outside of the Crater. And while previous research suggests that hyenas are the most conflict-prone large carnivores in the NCA (Dheer et al., 2021), the few detections of domestic animals here suggests that the majority of livestock depredation is conducted by non-Crater hyenas. It also suggests that domestic animals make up a small part of the diet of Crater hyenas, possibly because they are satiated by the Crater's abundance of wild prey. This is consistent with past research, which suggested that large carnivores only regularly consume domestic animals when wild prey is scarce (Khorozyan et al., 2015; Parsons, Newsome, & Young, 2022; Yirga et al., 2012). Altogether, our results suggest that the Crater hyena population is connected to those outside and that they rarely consume domestic animals.

Among wildlife species, wildebeest were the most strongly selected for, followed by Grant's gazelle and buffalo. This result is similar to that of Höner et al. (2002), a study which found that juvenile wildebeest, juvenile gazelles (both Grant's and Thomson's), and adult buffaloes were most strongly selected for. The similarity is noteworthy: the mentioned study was based on direct observations of hunts rather than on data collected from fecal samples. Thus, despite the methodological differences in the two studies, the five most commonly-detected species were the same. This indicates that DNA metabarcoding is likely an accurate way of assessing the diet of a given species. We caution, however, that our results cannot be assumed to be cases of predation, because DNA metabarcoding cannot differentiate between predation and scavenging. Thus, we only treat the detections of different species in our study as cases of hyenas consuming them (whether via predation or scavenging).

Finally, we found a strong, positive effect of age on the propensity to consume domestic animals. This may be because older hyenas are less likely to successfully hunt wild prey. Past reports of destroyed 'man-eaters' or 'problem animals' suggested that old large carnivores may be forced to rely feeding on domestic animals or humans due to age-associated physical decline (Rabinowitz, 1986). In contrast, other studies have suggested that conflict-prone individuals (at least in large felids; *Felidae* spp.) tend to be young, because they are transient and have not yet established territories with sufficient wild prey (Patterson et al., 2003; Woodroffe & Frank, 2005). This may be less likely in young hyenas, as females are usually resident in their natal clans for life, and most males disperse only as adults to the territory of a nearby clan (at around ~3.4 years old; Davidian et al., 2016; Davidian & Höner, 2022). Despite the significant positive association between age and domestic animal consumption, we acknowledge that our sample size was limited, with only 18 detections of domestic animals. Nonetheless, our finding warrants further research into the effects of individual socio-demographic traits on the consumption of domestic animals by large carnivores. This can inform evidence-based large carnivore conservation actions tailored towards preventing specific individuals from entering pastoralist areas.

Although management strategies tailored towards large carnivores in MUPA are lacking in robust scientific praxis, there is great potential for improvement. Our study used a rigorous method to assess the diet of hyenas to get answers to pressing conservation questions. We provide key information for applied ecologists and local authorities who aim to balance the needs of large carnivores, Threatened herbivores, and local communities. Our study also highlights how differences in anthropogenic influence create natural experiments that scientists can exploit to understand the behavior of keystone species in the Anthropocene. Further studies that rigorously assess diet to answer urgent conservation questions will identify finer-scale, best practices to bolster evidence-based large carnivore conservation.

5. Conflict of interest

The authors declare no conflict of interest.

6. Data availability

The authors will upload the data associated with this manuscript to Dryad following acceptance.

7. References

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Supplementary Material

DNA metabarcoding provides answers to key conservation questions about spotted hyenas

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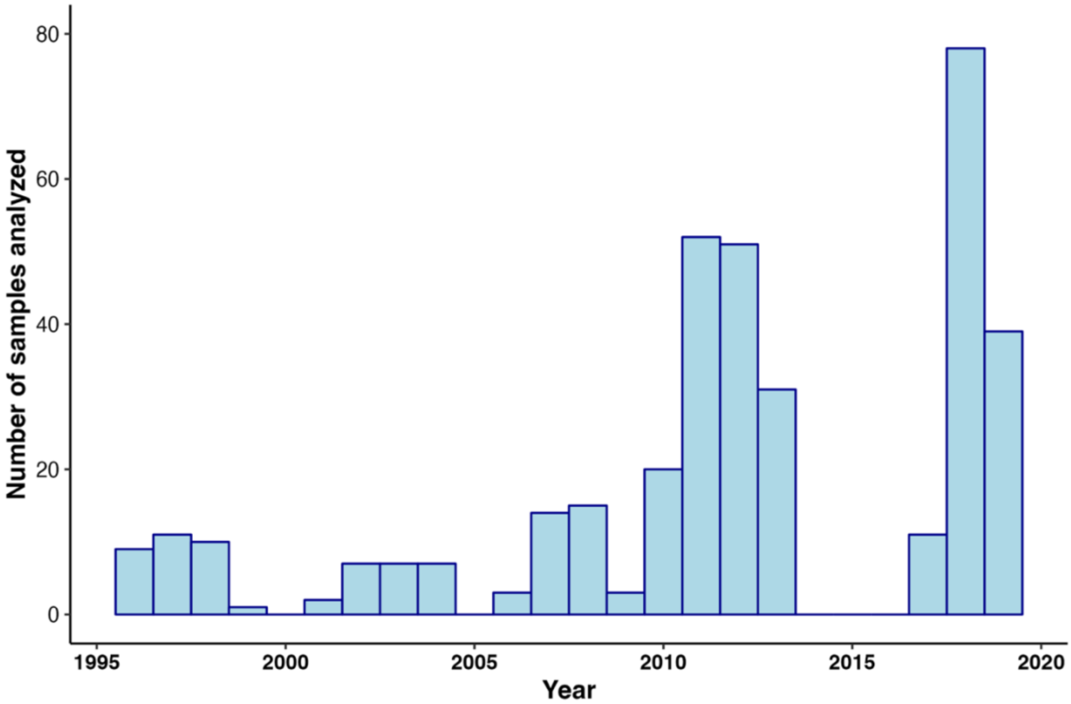

Figure S1: Histogram displaying distribution of fecal samples analyzed and included in this study by year. A total of 371 samples were analyzed for this study using DNA metabarcoding to assess the diet of spotted hyena clans resident on the floor of the Ngorongoro Crater, Tanzania.

Chapter 5

General discussion

This dissertation aimed to promote evidence-based large carnivore conservation and human-carnivore coexistence.

To meet this aim, I focused on three objectives: (i) identify the best predictors of the acceptance of large carnivore management strategies by local community members, (ii) assess the effects of anthropogenic activity on large carnivore fitness and physiology, and (iii) understand how large carnivores interact with Threatened wildlife and local communities in multi-use protected areas (MUPA). I combined socio-psychological data from the Ngorongoro Conservation Area (NCA) Maasai community with long-term data on the diet, fitness, and physiology of the free-ranging population of spotted hyenas in the Ngorongoro Crater. Using this interdisciplinary, modular approach allowed me to address each objective and meet my aim from multiple angles.

5.1 What are the best predictors of large carnivore management strategy acceptance?

Effective large carnivore management strategies require the acceptance of local communities (Dickman, 2010; Lindsey et al., 2013). A lack of this acceptance exacerbates conflict and hinders human-carnivore coexistence (see Treves & Santiago-Ávila, 2020). It is therefore important to know which strategies are most accepted, the factors that best predict acceptance, and how acceptance varies across species. So far, most research on management strategy acceptance has focused on livestock depredation as the main predictor of conflict and has been based on the perspectives of people in the Global North (see Chapter 2; also see Lozano et al., 2019). Recent studies, however, suggest that socio-psychological variables such as the emotions towards large carnivores and the cultural importance placed on them may also be strong predictors of management strategy acceptance (Jacobs et al., 2018; Lute & Attari, 2017). To facilitate human-carnivore coexistence, research that compares the predictive potential of livestock depredation and socio-psychological variables is needed, particularly in the Global South, where large carnivores are concentrated (Srivathsa et al., 2022).

In Chapter 2, I quantified the predictive potential of emotions, cultural importance, and livestock depredation on the acceptance of three management strategies often applied to mitigate human-carnivore conflict: no action, relocation, and lethal control. I interviewed 100 members of the Maasai community in the NCA. I used structured, closed questionnaires and focused on the three large carnivores involved in the most depredation regionally: hyenas, lions, and leopards.

My findings were consistent with the predictions that positive emotions and cultural importance are positively and negatively associated with protective and invasive management strategies, respectively. They were inconsistent with the prediction that livestock depredation would be a strong positive predictor of the acceptance of invasive strategies. Overall, protective strategies were mostly accepted whereas invasive ones were mostly rejected. Hyenas were viewed more negatively than both lions and leopards. Finally, livestock depredation by carnivores was a significantly smaller cause of livestock death than disease and drought were. The results suggest that socio-psychological variables may be more important predictors of management strategy acceptance than livestock depredation is, and that positive emotions might be stronger predictors than negative emotions are. They also indicate that there are major differences in how the Maasai community views different species within the large carnivore guild, and that disease and drought combined are a bigger source of damage to local livelihoods than large carnivores are.

5.1.1 The influence of socio-psychological variables

As predicted, the acceptance of management strategies was strongly influenced by two types of socio-psychological variables: emotions and cultural importance. Joy stood out as the strongest predictor; it had a positive effect on acceptance of no action and a negative effect on acceptance of relocation and lethal control. The effects of the positive emotion joy are consistent with previous findings that suggested that joy, an explicitly positive emotion, predicts a desire not to see animals harmed (see Chapter 2; also see Sponarski, Vaske, & Bath, 2015). Disgust had a weak effect and fear had no significant effect on the acceptance of management strategies. The effect of cultural importance was positive for no action and negative for relocation and lethal control, consistent with what I predicted.

These results underpin the substantial influence of affective and cognitive pathways in human-wildlife coexistence. It is important to consider the emotions that people feel towards large carnivores when seeking to establish coexistence between humans and these animals and promote evidence-based conservation. Evidently, people's emotions and cultural beliefs can play significant roles in shaping how likely they are to accept large carnivore management strategies. This builds on and is consistent with previous research that explored the relationship between socio-psychological variables and management strategy acceptance, including studies that took place in Europe, Asia, and other parts of sub-Saharan Africa (e.g.: Lischka et al., 2019; Jacobs et al., 2014; Sibanda et al., 2020; Struebig et al., 2018). Such cross-cultural similarities further underscore how crucial these variables are for applied ecologists and local authorities to consider. Adhering to this recommendation will be conducive to evidence-based large carnivore conservation and human-carnivore coexistence.

5.1.2 The influence of livestock depredation

Contrary to what I predicted, livestock depredation was only a significant predictor of the acceptance of relocation, and the relationship was negative. While this relationship may seem surprising given that Maasai pastoralists rely heavily on their livestock economically and for food security, there are multiple possible explanations. First, higher rates of livestock depredation may make the Maasai wary of management strategies like relocation, which risk having carnivores return again (Weise, Stratford, & van Wuuren, 2014). The relationship may also be influenced by the tourism industry, which provides considerable employment for Maasai community members and may mask the effects of livestock depredation (Melita, 2014). Previous research suggested that providing these economic benefits to local communities may ameliorate conflict (see Tchakatumba et al., 2019). It is also possible that the Maasai in the NCA are accustomed to livestock depredation and see it as a tolerable, ongoing, background event. Furthermore, it was a much smaller source of loss than disease and drought (see Chapter 2), which may mean they do not see it as a particularly rampant issue.

My findings suggest that livestock depredation might be overemphasized in human-carnivore coexistence research. This suggestion runs counter to the fact that many other human-carnivore coexistence studies emphasize livestock depredation as a substantial problem. Indeed, much of the literature has only or mostly focused on livestock depredation as a stand-alone issue and stressed the need to urgently quantify, prevent, and diminish it (e.g.: Abay et al., 2011; Kissui, 2008; Kolowski & Holekamp, 2006; Miller et al., 2016). This possible over-emphasis still occurs despite multiple studies which found that disease and drought kill substantially more livestock than large carnivores do (e.g.: Hazzah, Mulder, & Frank, 2009; Nyahongo & Røskaft, 2012; Rosas-Rosas, Bender, & Valdez, 2008), and those that cogently argue to consider the influence of socio-psychological variables (see Dickman, Marchini, & Manfredo, 2013; Jacobs et al., 2018). My study is thus the first to directly compare the predictive potential of livestock depredation and socio-psychological variables, and provides evidence that the latter may be the best predictors of large carnivore management strategy acceptance. Attaining human-carnivore may thus be far more complex than mitigating livestock depredation – both affective and cognitive pathways need to be considered.

5.1.3 Interspecific differences within the same guild

Though no action was mostly accepted and relocation and lethal control mostly rejected for all three carnivores, there were important differences across species. For example, the majority of respondents felt joy towards lions and leopards, but not hyenas. Furthermore, more respondents felt disgust towards hyenas than towards lions or leopards, and more respondents feared lions and leopards than hyenas. Respondents also found lions to be more culturally important than hyenas or leopards. Additionally, hyenas caused the most livestock depredation, followed by leopards and then lions.

My findings corroborate those of other studies which found major interspecific discrepancies in terms of both local community perceptions and livestock depredation (see Chapter 2; also see Mitchell et al., 2019; Parker et al., 2014). These results suggest that a large carnivore is not 'just' a large carnivore: there can be significant differences within the guild and it is advisable to consider this variation. Yet, many studies that assess local community perceptions towards and conflict with large carnivores take a single-species approach, even if multiple are present within the study area (e.g., studies that only focused on lion conflict in areas with other large carnivores: Bauer, de Iongh, & Sogbohossou, 2010; LeFlore et al., 2020; Lesilau et al., 2018; Saberwal et al., 1994). This narrow focus may overlook the nuanced relationships that people have with different large carnivores. By considering three species, three types of predictor variables, and three management strategies, my study therefore suggests that even though the strong influence of socio-psychological variables holds across species, there are still important differences in how people view the different species and how much livestock depredation each is responsible for. A broad focus may thus be conducive to holistic, evidence-based large carnivore conservation and human-carnivore coexistence.

5.1.4 Implications for studies on human-carnivore coexistence

The fact that emotions and cultural importance of large carnivores can strongly predict the acceptance of management strategies has major conservation implications. My findings suggest that local authorities should invest in outreach initiatives that focus on fostering positive emotions, such as joy, rather than addressing negative ones like disgust and fear. Education and awareness can promote positive emotions and improve knowledge of risks and conflict drivers, which can mitigate conflict. Charismatic species that are positively viewed, like lions, are more likely to evoke positive emotions, while less positively viewed species are more likely to elicit negative emotions. Depicting hyenas positively, for example, by highlighting their complex social behavior and their role in limiting the spread of disease, may reduce acceptance of relocation or lethal control. Outreach efforts that involve influential members of the community, such as elders, can also be effective in changing emotions towards carnivores. It is also important to collect long-term data on the cultural importance of large carnivores to identify shifts over time and how they affect acceptance of management strategies, and to consider species-specific differences.

On balance, the evidence suggests that there may be too much focus on livestock depredation in human-carnivore coexistence research. It is important for researchers to consider socio-psychological factors like emotions and cultural importance along with livestock depredation. Similarly, my study also suggests that disease and drought may need more focus than livestock depredation does. Further research on the acceptance of other management strategies, such as fortifying livestock corrals or compensation schemes, may also be useful in identifying the role that livestock depredation plays. Additionally, research investigating the interplay between the different variables tested in this study would be useful to identify whether, e.g., negative emotions might be an emergent property of severe livestock depredation. Such follow-up studies may glean insights that further support evidence-based large carnivore conservation and human-carnivore coexistence.

5.2 How does anthropogenic activity affect the fitness and physiology of large carnivores?

While the effects of anthropogenic activity on wildlife behavior are well-studied, its effects on fitness and physiology are not (Coetzee & Chown, 2016). Moreover, substantial changes to behavior are not always indicative of negative fitness or physiological effects, which are of greater conservation concern (López-Bao, Bruskotter, & Chapron, 2017). More knowledge of how anthropogenic activity affects fitness and physiology is needed in order to inform evidence-based conservation, especially for conflict-prone animals such as large carnivores. These effects may vary greatly based on how unpredictable and disruptive of critical behaviors the activity is, and the focal species' biology and social system (see Tablado & Jenni, 2017 for theoretical work).

In Chapter 3, I investigated how diurnal pastoralism affected the fitness and physiology of eight spotted hyena clans over a 24-year period within the Ngorongoro Crater. Using behavioral, physiological, and socio-demographic data from the clans, I exploited a natural experiment to compare the performance of clans exposed and unexposed to pastoralism. By assessing effects on fitness and physiology, I expanded on the substantial body of literature focused on behavioral changes and provided a new perspective by measuring fitness at the level of social groups. I also described how the effects of an anthropogenic activity may vary according to its predictability and disruptiveness, as well as the biology and social system of the study species. My study is therefore the first longitudinal assessment of how an anthropogenic activity affects the fitness and physiology of a group-living large carnivore population, and to measure these effects at the level of social groups.

My findings were inconsistent with the prediction that exposed clans would produce fewer juvenile recruits than unexposed clans would. They were consistent with the prediction that spotted hyenas from exposed clans did not have chronically elevated allostatic load, because fGMC were similar across the clan categories. I also found that exposed clans experienced less pressure from heterospecific competitors (lions), but enjoyed more prey than unexposed clans did. Overall, it was apparent that diurnal pastoralism did not pose a threat to the Ngorongoro Crater spotted hyena population.

5.2.1 Effects on fitness and physiology

Contrary to my prediction, exposed clans produced slightly more juvenile recruits per season than unexposed clans did, though the difference was not statistically significant. A GLMM confirmed that there was no significant difference in predicted juvenile recruitment between exposed and unexposed clans when controlling for other relevant variables. There were detectable effects of disease outbreaks (negative), the number of adult females in a clan (positive), and the lion index (positive) on juvenile recruitment. The effect of prey per capita was very small and not statistically significant. Moreover, I found that spotted hyenas in exposed clans had a very slightly, near-statistically significantly lower mean fGMC than those from unexposed clans. I also found no detectable difference in predicted fGMC between the two groups after controlling for other variables. Age had a weak, positive effect on fGMC. Clan size and rank had small, non-significant effects on predicted fGMC. Altogether, it was evident that diurnal pastoralism did not at all suppress the recruitment nor greatly elevate the allostatic load of spotted hyena clans.

These findings and the associated interpretation strongly contrast to those of many other studies that investigate the effects of anthropogenic activity on wildlife. In fact, much research implies, suggests, or concludes that anthropogenic activity is invariably bad for wildlife, especially for animals deemed susceptible to human-driven population decline and local extinction, such as large carnivores (Cardillo et al., 2004; Kuijper et al., 2016; Ordiz, Bischof, & Swenson, 2013). In my study, this was not the case: exposed clans performed just as well, if not even slightly better, than unexposed clans did. Studies may also make assumptions about the presence of conservation-relevant effects and threats to persistence simply due to detectable behavioral changes (see Baker & Leberg, 2018; Doherty, Hays, & Driscoll, 2021; Gaynor et al., 2018; but also see Beck, Lucash, & Stoskopf, 2009), which I contend might be presumptive. It is apparent that coexistence between anthropogenic activity and populations of group-living large carnivores is possible. To understand whether coexistence between an anthropogenic activity and the persistence of a given species is possible, studies should quantify effects on the species' fitness and physiology. Notwithstanding these arguments, the results from this chapter should be interpreted cautiously, and may be explained by the fact that the pastoralism was predictable and undisruptive to critical spotted hyena behaviors, the spotted hyena's biology and social system, and high prey availability in the Ngorongoro Crater.

5.2.2 The role of the type of activity, focal species biology and social system, and prey

In Chapter 3, I suggest that the effects of diurnal pastoralism on juvenile recruitment and fGMC in hyena clans could have been mitigated by factors such as the predictability and disruptiveness of the activity, the hyena social system, and the Ngorongoro Crater's consistently high prey abundance. First, the pastoralism occurred predictably and exclusively in the daytime, whereas spotted hyenas are mostly nocturnal foragers and can suckle very young cubs at night when exposed to pastoralism (see Kolowski et al., 2007). It follows that the pastoralism was undisruptive to critical behaviors, and my findings therefore support the idea that predictable, undisruptive activities may be conducive to coexistence with many species (e.g., southern giant petrel (*Macronectes giganteus*): Braun, Esefeld, & Peter, 2018; black grouse (*Lyrurus tetrix*): Immitzer, Nopp-Mayr, & Zohmann, 2014; Bornean orangutan (*Pongo pygmaeus*): Muehlenbein et al., 2012; bighorn sheep (*Ovis canadensis*): Wiedmann & Bleich, 2014). Additionally, my findings highlight the importance of considering the biology and social system of a species when investigating the effects of anthropogenic activity on wildlife (see Chapter 3; Berger-Tal & Saltz, 2016; Gittleman, 2019). The effects might have been much more negative if, for example, I had been monitoring a population of cooperative breeding large carnivores (e.g., African wild dogs (*Lycaon pictus*), which need sufficient 'helpers' to rear pups: Angulo et al., 2013; Somers et al., 2008). Finally, the role of prey abundance should not be overlooked: prey-rich environments such as the Crater allow female hyenas to produce sufficient milk for cubs (see Chapter 3; also see Wachter et al., 2002), which can facilitate juvenile recruitment. The consistently high prey abundance in the Crater and the recovering hyena population may also explain why there was no detectable effect of prey availability on juvenile recruitment, in clear contrast to studies suggesting that major fluctuations in prey availability strongly affect large carnivore fitness (e.g., cheetah (*Acinonyx jubatus*): Broekhuis et al., 2018; dhole (*Cuon alpinus*): Bhandari et al., 2021). Therefore, the consistently high prey abundance in the Crater may have been another factor that enabled coexistence between pastoralism and hyenas.

5.2.3 Implications for studies on the effects of anthropogenic activity on fitness and physiology

My findings in Chapter 3 have important implications for further research on the effects of anthropogenic activity on wildlife fitness and physiology. My results suggest that exposure to anthropogenic activity may not necessarily be detrimental to certain group-living species, particularly if the overlap between the species' critical behaviors and the activity is minimal. These results provide valuable insights for applied ecologists and local authorities who are working to strike a balance between the needs of local human communities and wildlife. Activities that have little overlap with the critical behaviors of target species may be encouraged or at least permitted. Longitudinal studies may then monitor how such activities are affecting the population. My results also highlight the great potential in viewing changes in anthropogenic activity as natural experiments to isolate and evaluate the way humans affect wildlife. However, to accurately disentangle the effects of localized anthropogenic activity from larger environmental patterns, such changes must be restricted to specific time periods and locations within a broader monitored area, as is the case in Chapter 3. More research is needed to better understand the effects of anthropogenic activity in light of different species and social systems, and to quantify effects on fitness and physiology. For instance, doing a similar study in an area with drastic fluctuations in prey availability, or on a species with a different social system, may reveal additional information as to how anthropogenic activity affects wildlife persistence. This can subsequently provide for evidence-based large carnivore conservation and human-carnivore coexistence.

5.3 How do large carnivores interact with Threatened wildlife and local communities in multi-use protected areas?

There is currently a lack of rigorous conservation research conducted in PA worldwide, which has led to faulty management decisions that hamstring evidence-based conservation and human-wildlife coexistence (Appleton et al., 2022; Sutherland, 2022). This is especially problematic for the management of MUPA, which are innovative experiments involving the cohabitation of local communities with wildlife (Searle et al., 2021). There is accordingly an urgent need to use rigorous techniques to gather robust evidence to answer important conservation questions in such mixed-use, shared landscapes (Maxwell et al., 2020; Naha et al., 2020). Robust evidence can help inform management strategies that balance the needs of local communities with those of wildlife and support effective management of MUPA. Gathering such evidence is especially important for wildlife of high conservation and management concern, such as large carnivores and Threatened herbivores (Bled et al., 2022; Bruskotter et al., 2017).

In Chapter 4, I used DNA metabarcoding of fecal samples to investigate the diet of the spotted hyena population in the Ngorongoro Crater over a 24-year period. The study aimed to answer questions about the spotted hyenas' interactions with Threatened wildlife species and the Maasai community in the wider NCA, including whether the spotted hyenas regularly consume black rhinoceros and if they forage in areas outside the Crater. I also examined the influence of individual socio-demographic variables (age, rank, and sex) on the spotted hyenas' propensity to consume domestic animals. My study thus represents the first robust, longitudinal assessment of large carnivore diet in a MUPA to answer pressing conservation questions related to their interactions with Threatened wildlife and local communities.

I found no detections of black rhinoceros DNA, which suggests that the spotted hyenas did not regularly consume them. I also show that hyenas at least occasionally left the Crater to forage, on account of multiple detections of both Maasai giraffe and domestic animal DNA. Furthermore, as I predicted, there was a significant positive relationship between age and the probability of a spotted hyena to consume domestic animals. There was no significant effect of rank nor sex, however, in contrast to my prediction.

5.3.1 Interactions with Threatened wildlife

In Chapter 4, I found no evidence of black rhinoceros DNA in 371 spotted hyena fecal samples collected over a 24-year time period. This suggests that the Crater spotted hyena population does not regularly consume black rhinoceros and does not pose a significant threat to the persistence of the Crater black rhinoceros population, a species of extremely high conservation priority to the Ngorongoro Conservation Area Authority (NCAA; the local governing authority) and other stakeholders (Mills et al., 2006; Moehlman, Amato, & Runyoro, 1996). Given the continuous, long-term alarm about large carnivore predation of both black and white rhinoceroses in sub-Saharan African PA (see Chapter 4; also see Berger, 1994; Fyumagwa & Nyahongo, 2010; Miller, 1987; le Roex & Ferreira, 2020; Sillero-Zubiri & Gotelli, 1991), my results may quell some fears. I recognize the possibility that spotted hyenas can prey on or scavenge black rhinoceros, but my study provides evidence that it is likely occasional at most, at least in the Crater. Furthermore, spotted hyenas likely struggle to take down well-armored, formidable, and massive herbivores such as black rhinoceros (Owen-Smith & Mills, 2008). Altogether, my study suggests that the Crater hyena population does not pose a credible conservation threat to the Crater rhino population.

5.3.2 Interactions with local communities

My results in Chapter 4 prove that Crater spotted hyenas occasionally consume Maasai giraffe. Additionally, the findings suggest that Crater spotted hyenas occasionally engage in depredation and/or scavenging of dead domestic animals outside the Crater. Overall, I found few detections of domestic animals, which suggests the Crater spotted hyenas likely have sufficient wild prey (Khorozyan et al., 2015). This indicates that the Crater may be ecologically sound in terms of wild prey abundance – large carnivores only tend to switch to regularly consuming domestic animals when wild prey reaches a critically low threshold (see Chapter 4; also see Chetri et al., 2019; Werhahn et al., 2019). The detections of Maasai giraffe and domestic animals also suggest that the Crater hyena population is connected to those outside, which is a positive sign of landscape connectivity and gene flow for this keystone, apex predator. Overall, my findings suggest that the Crater hyena population likely has sufficient wild prey, but that some individuals may occasionally leave the Crater and forage outside.

In Chapter 4, I also found that older age was associated with a greater probability of consuming domestic animals. Until now, there has been little focus on how individual socio-demographic traits influence the tendency of large carnivores to consume domestic animals (Morehouse et al., 2016). I provide evidence of this association and affirm previous suppositions about this relationship (see Chapter 4; also see Peterhans & Gnoske, 2001; Reza, Feeroz, & Islam, 2002). This study is, to my knowledge, the first to explicitly test for such a relationship using long-term data. Though my sample size was limited, the result paves the way for more research dedicated to investigating this relationship and preventing conflict by individuals that are likelier to enter human-dominated areas and consume domestic animals. Such conflict mitigation will bolster evidence-based large carnivore conservation and human-carnivore coexistence.

5.3.3 Implications for large carnivore management and diet assessments

Chapter 4 has implications for conservation management in the Crater and surrounding areas. First, the lack of black rhinoceros detections suggests that any potential management strategies tailored towards preventing spotted hyena predation of black rhinoceroses are at best unnecessary, and at worst, harmful. The fact that the Crater black rhinoceros population has consistently increased in size since the early 1990s indicates that it is likely secure, due to the efforts of the NCAA and a lack of predation pressure (Moehlman et al., 2020). Furthermore, Chapter 4 indicates that the Crater spotted hyenas are connected to populations outside and may occasionally consume domestic animals. They mostly consumed wild animals, which suggests that they likely have sufficient food within the Crater and do not need to rely on domestic animals. Comparative studies in other MUPA which have an intensively-protected area (such as the Crater) surrounded by human-dominated areas, will add to our knowledge of how spotted hyenas and other large carnivores use such shared landscapes.

I also found a positive association between hyena age and the consumption of domestic animals. If age is positively associated with the likelihood to consume domestic animals, management strategies may need to focus on preventing old individuals from entering human-dominated or pastoralist areas to prevent conflict. Additional research that accounts for how socio-demographic traits influence the propensity of large carnivores to consume domestic animals – and how to prevent it from happening – would thus be prudent. The intersection between such fine-scale behavioral research and conservation issues is termed ‘conservation behavior’ (Greggor et al., 2019) and needs further exploration to enable evidence-based large carnivore conservation and human-carnivore coexistence.

Finally, Chapter 4 also highlights the methodological value of using DNA metabarcoding to describe the diet of a given species, and its potential applications. I was able to verify the results from several samples, compare my results to those of a previous study based on direct observations (see Chapter 4, also see Höner et al., 2002), and answer important and straightforward conservation questions with this emerging molecular tool. Other diet studies can also yield important insights about large carnivore behavior in MUPA that will be of great value to applied ecologists, local authorities, local communities, and other stakeholders.

5.4 General conclusion

By demonstrating that emotions and cultural significance were much stronger predictors of acceptance of large carnivore management strategies than livestock depredation was, the dissertation suggests that conservation practitioners may focus too much on depredation as a barrier to coexistence. This is supported by the fact that disease and drought were much greater sources of livestock death than depredation was. Instead, practitioners may better prioritize eliciting positive emotions through community engagement, and take into account the varying views towards different species. In particular, I found that spotted hyenas were viewed less favorably than lions and leopards, but that invasive management strategies were not accepted for any of the species.

By showing that there was no detectable difference in juvenile recruitment (fitness) and allostatic load (physiology) between spotted hyena clans exposed and unexposed to diurnal pastoralism, the dissertation suggests that pastoralism had no major deleterious effect on the Crater spotted hyena population. These results imply that coexistence between humans and group-living large carnivores is possible if the overlap between the species' key behaviors and human activities is limited. The study also suggests that hierarchical social systems and abundant prey might buffer the effects of anthropogenic activity on group-living large carnivores and other species. Finally, it also offers a new approach to study human-wildlife interactions by measuring fitness at the level of social groups. This information is valuable for promoting human-wildlife coexistence in MUPA, conserving large carnivores, and monitoring fitness in group-living species.

By evidencing that the Crater hyenas did not regularly consume the black rhinoceros, the dissertation suggests that the Crater spotted hyena population does not pose a credible conservation threat to the Crater black rhinoceros population. The detections of Maasai giraffe and domestic animals show that the hyenas at least occasionally leave the Crater to forage, though they largely subsist on wild animals within the Crater. This suggests that the Crater spotted hyena population is likely satiated by the Crater’s consistently high prey abundance. Furthermore, the positive association between age and consumption of domestic animals has implications for conflict mitigation and emphasizes the importance of considering fine-scale socio-demographic variables to promote human-carnivore coexistence.

Additionally, the dissertation reinforces the value of using interdisciplinary, rigorous, and inclusive approaches when studying human-carnivore interactions. The research herein demonstrates the need to approach the human-wildlife nexus from multiple angles, use robust methods, and engage stakeholders in the process of identifying the causes, consequences, and mitigators of conflict.

Overall, this dissertation should contribute substantially to evidence-based large carnivore conservation and human-carnivore coexistence, particularly in MUPA and other mixed-use, shared landscapes.

5.5 References

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List of publications

†These authors contributed to this work equally

‡These authors supervised this work equally

Akash, M., **Dheer**, A., Dloniak, S., and Jacobson, A. (2021). The faded stripes of Bengal: A historical perspective on the easternmost distribution of the striped hyena. *European Journal of Wildlife Research*. DOI: 10.1007/s10344-021-01552-9

Braczkowski, A., Schenk, R., Samarasinghe, D., Biggs, D., Richardson, A., Swanson, N., Swanson, M., **Dheer**, A., and Fattebert, J. (2022). Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda. *PeerJ*. DOI: 10.7717/peerj.12307

Davidson, Z., Dupuis-Desormeaux, M., **Dheer**, A., Pratt, P., Doncaster, P., Chege, G., Mwololo, M., MacDonald, S., and Doncaster, C.P. (2019). Borrowing from Peter to pay Paul: Managing Threatened Predators of Endangered, Declining Prey Species. *PeerJ.* DOI: 10.7717/peerj.7916

Dheer, A. (2016). Resource partitioning between spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*). University of Southampton. *Master's thesis*. DOI: 10.13140/RG.2.2.16034.63689

Dheer, A., Davidian, E., Jacobs, M.H., Ndorosa, J., Straka‡, T.M., and Höner‡, O.P. (2021). Emotions and cultural importance predict the acceptance of large carnivore management strategies by Maasai pastoralists. *Frontiers in Conservation Science*. DOI: 10.3389/fcosc.2021.691975

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Montero-Mendieta[†], S., and **Dheer**[†], A. (2019). Digest: Resolving phylogenomic conflicts in characiform fishes. *Evolution*. DOI: 10.1111/evo.13666

Mwasi, S., and **Dheer**, A. (2022). Habitat degradation and wildlife-livestock interactions in Amboseli wildlife sanctuaries, Kenya. *African Journal of Ecology*. DOI: 10.1111/AJE.13048

Panda, D., Mohanty, S., Allen, M.L., **Dheer**, A., Sharma, A., Pandey, P., Lee, H., and Singh, R. (2022). Competitive interactions with dominant carnivores affect carrion acquisition of striped hyena in a semi-arid landscape of Rajasthan, India. *Mammal Research*. DOI: 10.1007/s13364-022-00663-1

C.V.

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Education

Leibniz Institute for Zoo and Wildlife Research & Freie Universität Berlin Berlin, Germany

Dr. rer. nat. Department of Evolutionary Ecology & Department of Biology, Chemistry, Pharmacy. Dissertation: Human-carnivore coexistence and the responses of spotted hyenas (*Crocuta crocuta*) to anthropogenic activity in Ngorongoro Conservation Area, Tanzania. 2017-2023 (expected).

University of Southampton Southampton, UK

M.Res. Wildlife Conservation. Centre for Biological Sciences, Faculty of Natural & Environmental Sciences. Thesis: Resource partitioning between spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) in Lewa Wildlife Conservancy and Borana Conservancy, Kenya. 2015-2016.

University of Maryland, College Park College Park, MD, USA

B.S. Environmental Science & Policy. Concentration: Wildlife Ecology & Management. College of Agriculture & Natural Resources. 2009-2013.

School for Field Studies Beverly, MA, USA

Undergraduate study abroad program focused on wildlife management in Lake Manyara ecosystem, Tanzania, and Amboseli ecosystem, Kenya. Independent research project: potential utility of the Grant's gazelle (*Nanger granti*) as an ecological bio-indicator for habitat quality. 2012.

Research Experience

Leibniz Institute for Zoo and Wildlife Research Berlin, Germany

Doctoral project focused on human-carnivore coexistence and the responses of spotted hyenas (*Crocuta crocuta*) to anthropogenic activity in Ngorongoro Conservation Area, Tanzania. Collected socio-demographic and behavioral data from spotted hyena clans resident in Ngorongoro and conducted questionnaires with the local Maasai community. Leveraged both local and international collaborations to meet project aims, conducted extensive science communication related to the study, and published cutting-edge research stemming from the fieldwork in high-ranking scientific journals. 2017-2023 (expected).

University of Southampton Southampton, UK

Master's project focused on dietary and spatiotemporal resource partitioning between spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) in Lewa Wildlife Conservancy and Borana Conservancy, Kenya. Spearheaded first ever collaring effort of spotted hyenas in Lewa and Borana, resulting in deployment of GPS-GSM collars on a total of seven spotted hyenas from five clans. Developed first ID database for the Lewa-Borana spotted hyena population. Also deployed collars on three lions from three prides. 2015-2016.

Brown Hyena Research Project Lüderitz, Namibia

Research assistant for long-term monitoring project on brown hyenas (*Hyaena brunnea*) along coastal Namib Desert, Namibia. Assisted with camera trapping, individual identification, telemetry, data entry, and provided support for graduate students involved with project. Researched and catalogued morphometric and skeletal data of over 40 individual brown hyenas. Also participated in outreach programs for local middle and high school students. 2014.

Botswana Predator Conservation Trust Maun, Botswana

Research assistant for multi-species large carnivore project, including spotted hyenas (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*), lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and leopards (*Panthera pardus*). Conducted direct and indirect behavioral research on all five species, including diurnal and nocturnal focal follows and camera trapping. Assisted with 4x4 Land Rover maintenance, camp upkeep, and graduate student projects as needed. Independently conducted telemetry in remote areas to locate collared individuals and gather observational data on hunting behavior, social behavior, and interspecific competition. 2013.

University of Maryland College Park, MD, USA

Laboratory assistant for long-term study on stalk-eyed fly (*Diopsidae*) evolution, sexual selection, and behavior. Responsible for feeding and cleaning of all cages for study populations. Assisted graduate students with research, data entry, laboratory maintenance, animal husbandry, and genetic techniques. 2013.

University of Maryland College Park, MD, USA

Analyzed video tapes of satin bowerbirds (*Ptilonorhynchus violaceus*) from Australia. Studied sexual selection, nesting behavior, and mating rituals and contributed to long-term research on this species. 2010.

School for Field Studies Beverly, MA, USA

Independent research project focused on examining the potential utility of the Grant's gazelle (*Nanger granti*) as an ecological bio-indicator of habitat quality in the Amboseli ecosystem, Kenya. 2012.

University of Maryland College Park, MD, USA

Compiled, transcribed, and entered observational data on a community of threatened and fragmented bird populations in Jamaica. Listened to audio tapes and developed an ethogram-based spreadsheet of foraging behaviors of different bird species, including bananaquit (*Coereba flaveola*), Jamaican woodpecker (*Melanerpes radiolatus*), and arrow-headed warbler (*Dendroica pharetra*). 2011.

Walter Reed Army Institute of Research Washington DC, USA

Led independent research project focused on amyloidosis, a rare disease characterized by build-up of proteins on tissues and organs. Wrote unpublished manuscript at end of 6-week internship. 2008.

Other Work Experience

Children Education Fund Nairobi, Kenya/Remote

Social media and fundraising coordinator for non-profit NGO dedicated to sponsoring secondary school education for talented Kenyan youth in five counties: Narok, Kajiado, Makueni, Machakos, and Kitui. Set up and ran all ex-situ project efforts. Collaborated with co-founders weekly to discuss project development, fundraising, and awareness. 2015.

Peer-reviewed publications

(* = co-first authors; + = co-senior authors)

Akash, M., **Dheer**, A., Dloniak, S., and Jacobson, A. (2021). The faded stripes of Bengal: A historical perspective on the easternmost distribution of the striped hyena. *European Journal of Wildlife Research*. DOI: 10.1007/s10344-021-01552-9

Braczkowski, A., Schenk, R., Samarasinghe, D., Biggs, D., Richardson, A., Swanson, N., Swanson, M., **Dheer**, A., and Fattebert, J. (2022). Leopard and spotted hyena densities in the Lake Mburo National Park, southwestern Uganda. *PeerJ*. DOI: 10.7717/peerj.12307

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Dheer, A., Davidian, E., Jacobs, M.H., Ndorosa, J., Straka+, T.M., and Höner+, O.P. (2021). Emotions and cultural importance predict the acceptance of large carnivore management strategies by Maasai pastoralists. *Frontiers in Conservation Science*. DOI: 10.3389/fcosc.2021.691975

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Montero-Mendieta*, S., and **Dheer***, A. (2019). Digest: Resolving phylogenomic conflicts in characiform fishes. *Evolution*. DOI: 10.1111/evo.13666

Mwasi, S., and **Dheer**, A. (2022). Habitat degradation and wildlife-livestock interactions in Amboseli wildlife sanctuaries, Kenya. *African Journal of Ecology*. DOI: 10.1111/AJE.13048

Panda, D., Mohanty, S., Allen, M.L., **Dheer**, A., Sharma, A., Pandey, P., Lee, H., and Singh, R. (2022). Competitive interactions with dominant carnivores affect carrion acquisition of striped hyena in a semi-arid landscape of Rajasthan, India. *Mammal Research*. DOI: 10.1007/s13364-022-00663-1

Selmoun-Ourdani, K., **Dheer**, A., Fritas S., Amroun, M., Zemmouri-Boukhamza, N., Mallil, K., and Wiesel, I. (TBD). Habitat suitability and road mortality of the striped hyena in Batna, Algeria. *Mammalia*. Under review.

Non-refereed publications

Dheer, A. (2016). Resource partitioning between spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*). University of Southampton. *Master's thesis*. DOI: 10.13140/RG.2.2.16034.63689

Journal Reviewer

African Journal of Ecology, Mammalian Biology, Oecologia, PeerJ, PLoS One

Posters, Talks, and Workshops

Dheer, A. (2012, May 1). “Potential utility of the Grant’s gazelle (*Nanger granti*) as an ecological bio-indicator for habitat quality”. Presented at School for Field Studies workshop with local community stakeholders, Kimana, Kenya.

Dheer, A. (2016, May 5). “Resource partitioning between spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*)”. Presented at Lewa Wildlife Conservancy community stakeholder meeting, Isiolo, Kenya.

Dheer, A. (2016, August 1), “Resource partitioning between spotted hyenas (Crocuta crocuta) and lions (*Panthera leo*)”. Presented as part of M.Res. degree requirements at University of Southampton, Southampton, UK.

Dheer, A. (2022, October 19). “Applied large carnivore research in Ngorongoro Conservation Area, Tanzania”. Presented as a guest lecturer at Macalester College, Saint Paul, Minnesota, USA.

Dheer, A. (2022, November 9). "Diurnal pastoralism does not reduce juvenile recruitment nor elevate allostatic load in spotted hyenas". Presented at The Wildlife Society Conference in Spokane, Washington, USA.

Dheer, A. (2018, June 18). "Management of spotted hyenas in Ngorongoro Conservation Area". Presented at Large Carnivore Conservation Workshop for Ngorongoro Conservation Area Authority, Karatu, Tanzania.

Dheer, A. (2019, February 13 & 2019, October 8). "Ngorongoro Hyena Project: ecology, evolution, and conservation of a keystone large carnivore". Presented as a guest lecturer to School for Field Studies students and staff, Rhotia, Tanzania.

Dheer, A. (2019, June 7-12). "IUCN Hyaena Specialist Group Workshop". Attended and participated in workshop with other scientists researching *Hyaenidae* species. Ongava Research Centre, Namibia.

Dheer, A. (2019, June 9). "Adaptability of spotted hyenas to anthropogenic change and human carnivore-conflict". Presented doctoral project outline to other members of IUCN Hyaena Specialist Group at Hyaena Distribution Mapping Project Workshop. Ongava Research Centre, Namibia.

Dheer, A. (2019, September 26). "Social media as a tool for early career scientists". Led workshop at 2019 IZW PhD Student Symposium, Berlin, Germany.

Dheer, A., Davidson, Z., Doncaster, C.P., Dupuis-Desormeaux, M., MacDonald, S., Chege, G., and Mwololo, M. (2016, 2017). Resource partitioning between spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*). EAZA Annual Conference, Belfast, Northern Ireland and the 11th International Conference on Behaviour, Physiology, and Genetics of Wildlife, Berlin, Germany. Poster.

Dheer, A., Straka, T., Jacobs, M., & Höner, O.P. (2019, October 1). "Maasai-carnivore interactions in Ngorongoro Conservation Area, Tanzania". Talk given at 2019 Wildlife Research Conference, Berlin, Germany.

Dheer, A., Straka, T., Jacobs, M., & Höner, O.P. (2020, February 18). "Understanding Maasai-carnivore relationships in Ngorongoro Conservation Area, Tanzania". Talk given at 2020 Pathways Conference, Limuru, Kenya.

Science Communication

Caruso, N., and Rabaiotti, D. (2017, October 19). Contributor to best-selling humorous book about animal flatulence titled "Does It Fart?". *Quercus Books*.

Cheruto, N. (2022, August 11). Interviewed for article "From the Field: An interview with Arjun Dheer". *WILDLABS.NET*.

Dell'Amore, C. (2019, June 15). Interviewed for article "Hyenas have a bad rap—but they're Africa's most successful predator". *National Geographic*.

Dheer, A. (2013, December 8). Wrote article “David and Goliath in the Wild”. *The Zambezi Traveller* 15, 42.

Dheer, A., Edwards, S., Murray, E., and Shikongo, F. (2014, May 22). Participated in Lüderitz High School outreach program about carnivore ecology and conservation for International Day for Biological Diversity in collaboration with Ministry of Environment and Tourism. Lüderitz, Namibia.

Dheer, A., and Naman, P. (2022, November 10). Co-wrote Swahili-language article “Kuishi pamoja kunawezekana” for Tanzanian science newspaper *MwanaSayansi* 3, 4.

Distefano, C., and Pappas, Y. (2019, September 18). Interviewed for comedy podcast episode titled “Hyena Experts are Wild!” *History Hyenas*.

Engh, B. (2017, February 18). Wildlife photography featured in educational YouTube series “Dinosaurs of Copper Ridge”. *Brian Engh Paleoart*.

iNaturalist (2020, June 11). Led breakout session for webinar “National Geographic Introduction to iNaturalist Webinar” and instructed fellow National Geographic Explorers on how to use iNaturalist for research purposes.

Japan Broadcasting Corporation/NHK (2019, October 21). Participated in filming of “Learning The System” episode of Japanese TV series “Darwin’s Amazing Animals”.

Kinuthia, W. (2017, June 12). Master’s research featured in “Lewa Wildlife Conservancy Impact Report 2016”. *Lewa Wildlife Conservancy*.

Klein, J. (2017, January 13). Interviewed for article “Sometimes Nature is Morbid. That’s Why There’s #BestCarcass”. *The New York Times*.

Litton Weekend Adventure (2019, February 3). Doctoral research featured as focus of 30-minute 3rd season finale of Emmy Award-winning TV show “Ocean Treks with Jeff Corwin”.

Marwell Wildlife (2016, July 20). Master’s research featured in article “Conservation for the Future”. *Marwell News*, 77.

National Geographic Society (2021, March 11). Participated in “Show and Tell” symposium sharing PhD research with other National Geographic Explorers across Europe and Africa.

National Geographic Society (2021, June 14-18). Participated in “Explorer Festival” to share and collaborate on research efforts with fellow National Geographic Explorers.

National Geographic Society (2021-2022). Selected for and participated in “Explorer Educator Exchange” program, involving outreach with high school (age

14-18) students in Center Valley, Pennsylvania, to present on and discuss about wildlife research, careers in science, and pressing conservation issues.

National Geographic Society (2023, April 24 & 27). Selected for and will participate in “Explorer Classroom” program, involving discussions about large carnivore ecology and conservation with grade school (ages 4-14) students.

Reese, B. (2019, September 10). Interviewed for podcast episode titled “Ecology, Evolution, and Conservation of Large Carnivores”. *The Bus Driver Experience*.

Reye, B. (2018, July 6). Interviewed about PhD research for article “Die Chefinnen der Savanne”. *Tagesanzeiger* & *Der Bund*.

Rust, N. (2018, February 14). Interviewed for article about spotted hyenas “Brains and Brawn”. *BBC Wildlife Magazine 36(3)*, 47-50.

School for Field Studies (2019, March 13). Selected to be featured on School for Field Studies website under *Alumni Stories* section. https://fieldstudies.org/alumni/alumni-stories/arjun-dheer/

Stacey, Katie. (2019, September 24). Interviewed for article “Hippo and hyena touch noses in rare encounter”. *National Geographic*.

Wiesel, I. (2014, June 30). Article featured in section of project newsletter. *Brown Hyena Research Project Newsletter 46*, 4-5.

Wiesel, I. (2014, September 30). Article featured in section of project newsletter. *Brown Hyena Research Project Newsletter 47*, 2-3.

WILDLABS.net (2018, March 1). Received 2nd place award for #Tech4Wildlife Photo Challenge on Twitter featuring fieldwork on spotted hyenas and lions in Kenya, amongst hundreds of entries.

Twitter: @ArjDheer (4,653 followers); @HyenaProject (7,755 followers); @HyaenaSpecialistGroup (498 followers)

Instagram: @ArjDheer (2,515 followers); @HyaenaSpecialistGroup (1,839 followers)

YouTube: HyenaProject (41,100 subscribers)

Facebook: HyaenaSpecialistGroup (3,200 followers)

Awards, Scholarships, and Grants

- Leibniz Open Access Fund (2021; $1,150)
- Experiment DNA Metabarcoding Campaign (2019; $4,522 (107% of target))
- IZW Metabarcoding Grant (2019; €3,500 ≈ $4,150)
- National Geographic Early Career Grant (2017; $4,905)

- IDEA WILD Equipment Grant (2017; $212)
- IUCN/SOS Threatened Species Grant (2017; €35,000 ≈ $41,150)
- IZW Doctoral Scholarship (2017; ~€58,500 ≈ $62,100)
- University of Maryland Honors Program Citation (2013)
- School for Field Studies General Scholarship (2011; $3,000)
- University of Maryland Dean's List (2011)
- University of Maryland President's Scholarship (2009; $12,500)
- AFSA/Turner C. Cameron Memorial Academic Merit Scholarship (2009; $2,500)
- National Merit Commended Student (2008)

Activities and Memberships

University of Maryland Terrapin Trail Club, 2010-2013

University of Maryland Wildlife Society, 2013

Student Representative for University of Southampton Graduate School Committee, 2015-2016

University of Southampton Biological Science Postgraduate Society, 2015-2016

Society for Conservation Biology, 2017-present (Africa Section)

IUCN SSC Hyaena Specialist Group, 2017-present (Member 2017-2021, Red List Authority 2021-present)

5th IZW PhD Symposium Committee, 2018-2019

The Wildlife Society, 2017-present

National Geographic Explorer, 2018-present

Certifications and Courses

Driving License (Maryland, USA), 2008

IUCN Global and Regional Red List Assessor, 2016

IZW "Solving problems in biostatistical analysis and experimental design in the life sciences" course, 2017

IZW "Theory of Science I & II" course, 2020

IZW "How to Write a Scientific Paper" course, 2021

National Geographic "Introduction to Conservation" course, 2020

National Geographic "Understanding Illegal Wildlife Trade" course, 2020

Languages

Native proficiency: English

Professional working proficiency: Swahili

Elementary proficiency: Punjabi, Hindi

References

Available upon request