Received: 3 May 2024 | Revised: 6 November 2024 | Accepted: 16 December 2024

DOI: 10.1111/csp2.70001

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access
WILEY

CONTRIBUTED PAPER

The benefits of inclusive conservation for connectivity of lions across the Ngorongoro Conservation Area, Tanzania

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Funding information
NABU (The Nature And Biodiversity Conservation Union); Global Conservation; Lincoln Park Zoo; Lion Guardians; PAW Foundation; National Geographic Society, Grant/Award Numbers: B15-15, B4-17, NGS-85137C-21, W235-12; SOS-IUCN Save Our Species, Grant/Award Number: 2021A-6; Wildlife Conservation Network's Lion Recovery Fund, Grant/Award Numbers: TZ-KL-01, TZ-KL-02-LRF, TZ-KL-03-LRF, TZ-KL-04-LRF, TZ-KL-05-LRF; Donald Slavik Family Foundation; World Wildlife Fund, Germany, Grant/Award Number: 14810/BBR; Maliasili; Panthera; MilkyWire; Wildaid

Abstract

Human impacts on the planet degrade natural habitats, often restricting wildlife to protected areas. If connectivity between such areas is lost, wildlife populations may lose genetic diversity, thereby increasing extinction risk. For large carnivores, connecting populations separated by human-occupied habitats requires dedicated effort to foster human–wildlife coexistence. Using lion observation data from 1962 to 2023 and movement data from GPS collars, we evaluated how inclusive conservation actions (i.e., directly involving local communities) in the Ngorongoro Conservation Area (NCA), Tanzania, are affecting the ability of lions to use and traverse human-occupied habitats. Efforts to promote human–lion coexistence were positively associated with the number of lions moving across human-occupied habitats and the ability of lions to settle in human-occupied areas, suggesting that conservation activities are having the desired impact on connectivity. However, despite a reduction in negative human–lion interactions from 2016 to 2021, the number of retaliatory lion killings and livestock attacks both increased sharply during an extreme drought in 2022, before dropping again in 2023. Thus, although our results highlight the benefits of inclusive conservation for connectivity of large carnivore populations, recent events highlight continued challenges and the need for long-term, nimble approaches to maintain balance where humans and large carnivores coexist.

KEYWORDS

community engagement, conservation efficacy, habitat connectivity, human–wildlife coexistence, human–wildlife conflict, large carnivore, *Panthera leo*

1 | INTRODUCTION

As the human population of the planet rises, natural habitat is lost and wild animal species are increasingly restricted to protected areas in small, insular populations (Diamond, 1975). The small size and isolation of these populations can lead to more rapid loss of genetic diversity (Leroy et al., 2018), potentially reducing individual fitness via inbreeding depression, emergence of large-effect deleterious mutations, and loss of adaptive potential (Frankham, 1996; Leroy et al., 2018). Reduced fitness, an inability to respond adequately to environmental fluctuations and inherent demographic stochasticity put small, isolated populations at high risk of extinction (Lacy, 1987; Soule, 1976). To prevent the isolation of animal populations, promote genetic diversity, and reduce extinction risk, conservation efforts have focused on landscape connectivity to facilitate the free movement of animals among otherwise detached subpopulations (Tewksbury et al., 2002). For wide-ranging species, achieving landscape connectivity is especially difficult, requiring the establishment of extensive corridors that provide safe routes of travel to increase immigration rates (Simberloff et al., 1992). However, the effectiveness of such corridors is variable and often subject to human impacts, especially for species for which negative human–wildlife interactions are common (Cushman et al., 2018).

Lions and humans in Africa have a long history of negative interactions, with lions preying upon livestock and sometimes killing people, resulting in retaliatory killings aimed at preventing further loss of life and livelihood (Kissui, 2008; Packer et al., 2019; Patterson et al., 2004). Habitat loss, retaliatory killings, and bushmeat poaching that deplete the lion's natural prey base have led to decreases in lion population prevalence and size across their range (Bauer et al., 2022; Loveridge et al., 2022) with remaining populations surviving best in protected areas sheltered from human persecution (Lindsey et al., 2017; Packer et al., 2013). Connectivity between protected areas for lions is male-mediated via dispersal of young nomads or displaced territorial males (Elliot et al., 2014; Packer, 2023), with females being predominantly philopatric (Curry et al., 2021; Dures et al., 2021; Packer, 2023). However, most protected areas are isolated and surrounded by human-occupied landscapes, making dispersal difficult or impossible (Cushman et al., 2018), resulting in significant genetic isolation across the African lion's range over the last 30 years (Curry et al., 2021).

One of the most well-studied populations of African lions resides in the Ngorongoro Crater, Tanzania (hereafter "Crater"). Studied in detail for over 60 years, the Crater population is known for its relatively low genetic diversity resulting from limited connectivity with other lion populations, and disease-induced population bottlenecks (Jansson, 2024; Packer et al., 1991). Following a crash in 1962, the population subsequently recovered with the addition of numerous males that were able to immigrate into the Crater. However, little further immigration occurred in the following two decades at which point high levels of inbreeding were apparent with abnormal sperm, low heterozygosity, and low reproductive success (Packer et al., 1991). Furthermore, high levels of inbreeding were thought to contribute to increased susceptibility to disease, evidenced by high mortality during three disease outbreaks between 1994 and 2001, after which the population was unable to recover to previous levels (Kissui & Packer, 2004). This has prompted efforts to increase genetic diversity by enhancing the connectivity of the Crater population with lions inhabiting the Serengeti National Park (hereafter "Serengeti"), ~50 km to the northwest. If Serengeti lions can successfully disperse into the Crater population, then genetic diversity may be increased (Mech & Hallett, 2001). However, such dispersals would require navigation of the Ngorongoro Conservation Area (hereafter "NCA"), a multi-use landscape allowing pastoralists to live and herd livestock among wildlife. Importantly, there are no structural limitations to lion dispersal through the NCA (Jansson et al., 2024), with connectivity limited only by negative interactions with humans. Thus, such multi-use landscapes are increasingly recognized as critical areas for the conservation of large carnivores, with success relying on behavioral adaptation of both people and carnivores (Carter & Linnell, 2016). Here, we define "coexistence," following Carter and Linnell (2016), as a dynamic, sustainable state in which humans and large carnivores adapt to living together, promoting long-term carnivore population survival, social acceptance, and tolerable levels of risk. As of 2020, the human population of the NCA was approximately 100,000 people (~13 km^{-2}), having increased at least 5-fold since 1979 (IUCN, 2020). Although lion dispersal through human-occupied landscapes has been achieved in other areas of Africa (Dolrenry et al., 2020; Matshisela et al., 2022), dedicated efforts to increase tolerance, mitigate negative interactions and prevent retaliatory and ritual killings are required to foster human–lion coexistence (Sibanda et al., 2022; Western et al., 2019).

REDACTED is an NGO operating in the NCA to support human–lion coexistence via inclusive conservation, implementing and adapting the Lion Guardians Model (Dolrenry et al., 2016), originally developed in the Amboseli-Tsavo Ecosystem, Kenya. Inclusive conservation incorporates the voices and direct involvement of local communities in the protection and management of nature (Tallis & Lubchenco, 2014; Young et al., 2021). Involving local communities in conservation efforts has been associated with decreases in persecution of large carnivores, with benefits for large carnivore abundance (Nawaz et al., 2008) and occupancy of human-dominated areas (Schumann et al., 2008). The Lion Guardians Model approaches inclusive conservation by employing local traditional warriors to work directly in their home communities promoting human–lion coexistence, using their local knowledge and relationships to protect people, livestock, and lions. While this model has been used in other regions of Africa, the success of such a program has never been evaluated in terms of fostering connectivity of lion populations separated by human-occupied areas. The objectives of this study are to evaluate if inclusive conservation activities are promoting movement of lions into the Crater from outside areas, and the ability of lions to move through and occupy the greater NCA landscape. If conservation efforts in the NCA are improving connectivity between the Crater lions and lion populations inhabiting the NCA and beyond, we make three predictions: (1) there will be an inverse relationship between conservation efforts and negative human–lion interactions (i.e., lion killings, livestock losses due to lions relative to number of lions over time), (2) lion dispersals into and out of the Crater will be positively associated with conservation efforts over time, and (3) the ability of lions to use human-occupied areas without being killed has increased over time following the initiation of conservation activities in the NCA.

2 | METHODS

2.1 | Study area

The NCA encompasses ~8300 km^2 including the Ngorongoro Crater in the east, stretching westward to Serengeti National Park. Although the NCA is a component of the Greater Serengeti Ecosystem, it is unique in allowing traditional pastoralism (i.e., a multi-use protected area) where the majority of NCA land is accessible for grazing and settlement by residents and their livestock, but not for cultivation or construction of permanent infrastructure. The NCA multi-use area (hereafter "greater NCA") connects the small, high-density lion subpopulation of the Ngorongoro Crater with the extensive Serengeti lion population. Portions of the NCA have prohibited pastoralism (i.e., are wildlife-only zones), and since 2017 this includes the Crater floor itself, the floors of two other nearby craters, the eastern highland forest, and the western section of Ndutu, at the Serengeti border (Figure 1). Ndutu is a heterogeneous area of woodlands, soda-lakes, and marshes surrounded by the vast short-grass plains that straddles the NCA and Serengeti boundaries. Ndutu is a particularly important area for lion connectivity between the Serengeti and the Crater (Figure 1), supporting diverse and abundant wildlife populations, including lions, and representing the most immediate source of lion immigrants into the Crater.

The NCA landscape is a mix of forested highlands, rugged escarpments, volcanic calderas, *Acacia* and *Commiphora* woodland savannah, and vast open grasslands. Altitudes range between 1000 and 3000 masl, and rainfall from 400 to 700 mm year^{-1}. The NCA exhibits wet and dry seasonality, with good wet-season grazing for both wildlife and livestock between December and May, and increasingly limited dry-season grazing between June and November (Metzger et al., 2015). During the dry season, water is scarce, with most rivers being seasonal and many water-bodies undrinkable due to very high soda/salt levels. Consequently, wild herbivore abundance is low during the dry season and pastoralist movements widen in search of the limited pasture. However, pastoralist movements remain constrained by water availability in both seasons, and have become increasingly sedentary over time (Homewood et al., 2009). When the rains arrive, vast herds of migratory herbivores, including ~1.3 million wildebeest (*Connochaetes taurinus*) (Sinclair et al., 2015), return to the short-grass plains. Between January and April, during the wildebeest's synchronized calving (Estes, 1976), pastoralists remove their cattle herds from the grasslands to avoid infection from the Malignant Catarrhal Fever virus (Cleaveland et al., 2023; Plowright 1965). This creates a period of separation of livestock from wildlife on the grasslands in the wet season, which then host abundant wildlife (Ikanda & Packer, 2008).

2.2 | Promotion of human–lion coexistence

We began community engagement activities in the NCA in 2011, hiring individuals from the local communities to expand lion monitoring and record lion-livestock attacks. In 2014, we began formally implementing the Lion Guardians Model (Dolrenry et al., 2016), forming the *Ilchokuti* ("guardian" in the Maa language) program. Ilchokuti are pastoralists and may have previously participated in lion hunts, recruited based on an interest in wildlife conservation and demonstrated high local ecological knowledge. Ilchokuti use their skills (i.e., "reading" animal tracks, local ecological knowledge) to monitor lions and may also assist in monitoring patterns and intensities of livestock losses due to lions. No

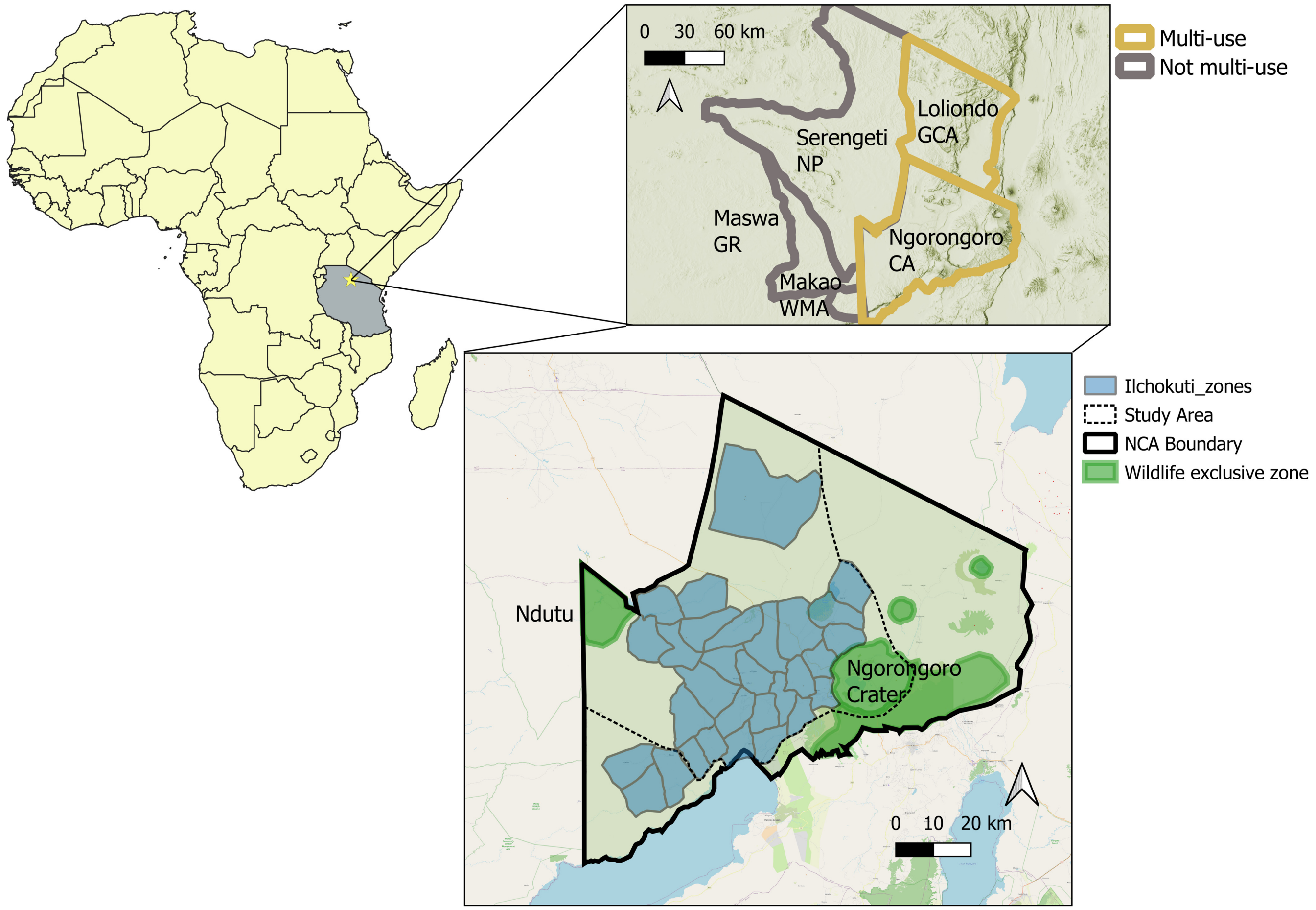

FIGURE 1 Ngorongoro Conservation Area (NCA) and the Greater Serengeti Ecosystem, Tanzania. The dark green sections denote areas in the NCA where pastoralist activity is not permitted, including the Ngorongoro Crater, western part of Ndutu, and eastern Highland forest. The remainder of the NCA is open to pastoralist use. Data on lions were gathered throughout the study area, with regular monitoring of the lions in the Ngorongoro Crater and Ndutu. The blue polygons denote the zones where each Ilchokuti (guardian) conducts his outreach and activities to promote human–lion coexistence.

compensation is offered in the NCA for losses caused by wildlife, hence there is no obvious incentive for over-reporting attacks. Ilchokuti are well respected within their communities, leveraging their local network to work as lion ambassadors, protecting lions by keeping people and livestock safer. Regular duties to promote human–lion coexistence include wound treatment of livestock injured by carnivores, reinforcement of bomas (i.e., a pastoralist homestead with protective corral), retrieval of lost livestock and telemetry tracking of GPS collared lions for an early warning to communities of lion presence in the area. The Ilchokuti are also well-placed to prevent and/or stop hunts of lions by peers, through suggesting alternate activities, using techniques to calm aggression, preventing physical access to a lion, and rebuilding support for lion protection following an attack. However, tracking of lion hunts and the number of lions killed is difficult, and we consider our data on these variables to represent minimum counts only. In areas and periods of heightened negative interactions, we arrange for additional Ilchokuti presence and efforts to protect lions and support human–lion coexistence.

2.3 | Lion monitoring

2.3.1 | Crater and Ndutu

The demographic study of Crater lions was started by the Serengeti Lion Project (Packer, 2023) in 1974, using regular, visual observations and individual identification of all lions on the Crater floor. Prior demographics, back to 1962, were reconstructed using photo observations (Packer et al., 1991). Monitoring of Crater lions has continued to present with a consistent effort and protocol, and expanded to Ndutu, including collection of photographic data since 2007 and initiation of regular visual monitoring in 2010.

We monitored lions 3–5 days per month in the Crater (250 km^2, with roughly 50% of the area accessible for monitoring) and 2–6 days per month in Ndutu (approximately 400 km^2, all accessible), using a vehicle, searching widely in each area by scanning viewsheds and targeting lion-preferred habitats (e.g., drainages, hills, tree clumps). Lions are identified using natural markings (e.g., whisker spot pattern, scars) (Pennycuick & Rudnai, 1970). We match each individual against known individuals in our lion database, allowing us to identify when new cubs were born or when new adults/subadults entered an area. While lions are readily detectable in the Crater, Ndutu is more challenging given the greater extent of woodland brush that reduces the detection of lions. Thus, we supplemented Ndutu monitoring with photos and information collected by two tour guides and a few returning visitors, whose contributions remained relatively consistent throughout the course of the study.

We created a monthly index of lion abundance in the Crater and Ndutu as the minimum number of lions known or assumed alive each month, with this number likely representing a near-total count in the Crater. Adult lions (≥2 years old) were assumed alive if observed in the last 6 months while juveniles and cubs were assumed alive if regularly seen in their mothers' company. For a given year, we report the single highest count observed between two census dates: 1 January and 1 July.

2.3.2 | Greater NCA

The monitoring of lions in the greater NCA (i.e., multi-use areas excluding the Crater and Ndutu) is challenging, given inaccessible terrain, low lion densities, and more elusive lion behaviors. While individual identification of uncollared lions in the NCA is attempted following reports of lions in an area, most remain unidentified. Most observations of lions in the greater NCA are collected by Ilchokuti, using regular surveys over the zones in which they live (Figure 1). The Ilchokuti perform their surveys on foot, recording date and GPS location for any observations of lions visually or from signs (tracks, scat, hair). They also record the number of lions in a group, age-cohort, and sex if possible.

2.4 | Lion movement

To understand movement behavior by lions through the greater NCA, we deployed GPS collars on 25 individuals (10 females and 15 males) from 2012 to 2023, with a maximum of six lions collared simultaneously. On average, individual lions were collared for 18.9 months (range: 2.1–66.0 months) with nine lions being collared for 2 years or more. We used GPS Plus and Vertex Lite (Vectronic Aerospace) GPS-collar models with Iridium satellite transmission, VHF-beacon, and remote drop-off function, and scheduled the collars to take positions every 1–2 h, day and night. The collar batteries lasted for 2–3.5 years, after which the collar was either removed (using remote drop-off) or replaced. Based on our knowledge of the usual range of their pride or coalition, we prioritized collaring adult lions of either sex, focusing on areas and individuals where we expected a high risk of negative human–lion interactions. Apart from studying lion behavior through fine-scale movements, the collars served as an early-warning system of lion presence to livestock herders in the area.

Lions in the greater NCA are few and elusive, hence immobilization to deploy collars is challenging and performed opportunistically and mainly at night. To attract shy lions to the vehicle for immobilization, we broadcasted a high-volume recording of feeding hyenas, a bleating buffalo calf, or the roars of an unfamiliar lion. The lions were collared with permission from the Tanzania Wildlife Research Institute and the Ngorongoro Conservation Area Authority, whose veterinarians immobilized and supervised the collaring of all animals. Lions were immobilized using a dart-gun from a vehicle at 10–20 m distance, and collars were fitted by an experienced field researcher. We then stayed close to the lion until it recovered from the immobilization.

2.5 | Lion exploitation of human-use areas over time

We assessed whether lion use of the greater NCA (i.e., multi-use habitat) changed over time using three sources of data described above: observations of individually identified lions (primarily in the Crater and Ndutu), movement data from GPS collared lions, and lion observations from the greater NCA (without individual identification).

2.5.1 | Lion observations (individual IDs)

Using the lion observation data in the Crater and Ndutu between 2013 and 2023, we visualized the frequency with which individual lions were observed outside of their natal area (i.e., Crater or Ndutu). We also used a mixed logistic regression via the glmer routine in program R (R Core Team 2021) to model whether the probability of a Crater-born lion leaving its natal area at least once (within a given year) increased over time. We weighted our analysis based on the total number of lion observations (including all individuals) recorded outside the Crater each year, since the effort expended will affect the ability to detect Crater-born lions outside of the Crater. We included a random effect for lion ID to account for some lions being more philopatric than others. In Ndutu, since the area is larger, more forested than the Crater and contiguous with the Serengeti, it is more challenging to locate the lions, obtain regular sightings, and identify where they go when they leave. Thus, we were unable to statistically assess the probability of lion movements outside of Ndutu.

2.5.2 | GPS tracking

Using data from lions that were fitted with GPS collars, we assessed the number of steps taken by each animal (relative to the total number of steps recorded for that animal) that were outside the area where the lion was collared (i.e., lions that moved from the greater NCA into the Crater or vice versa). Using a mixed logistic regression via the glmer routine in program R with a random effect for each lion, we tested whether the average rate of movement outside of the original collaring area (in either direction) has changed significantly over the time of conservation activities.

We also assessed whether dispersing males were able to settle in the greater NCA, as inferred from any shift in the minimum convex polygon containing all GPS locations over each year of conservation activities. We used a mixed Poisson regression with year as the sole fixed effect and lion ID as a random effect, with the log of the number of GPS locations taken in a year used as an offset.

Finally, because of the distinct contrasts between the dry and wet season in human activity, prey availability, and habitat use, we tested whether the proportion of total lion movements for collared animals that were located in the greater NCA differed with season using a mixed logistic regression with season as the sole fixed effect and lion ID as a random effect.

2.5.3 | Lion observations (no individual IDs)

Since lion identification in the greater NCA is challenging, we used Ilchokuti observations to calculate a rough index of lion abundance each year from 2015 to 2023. This index was calculated as the mean number of monthly lion observations each year collected by each Ilchokuti within his/her working zone and represents changes in relative lion activity over time in the greater NCA. We modeled annual changes in this index using a Poisson regression, with the log of the total number of square kilometers monitored each year as an offset to account for effort and year as the sole fixed effect. We also assessed changes in the area over which pastoralists reported lion attacks by bounding all report locations within a given year by a minimum convex polygon. We then modeled changes in polygon area over the years from 2015 to 2023 using a Poisson regression with year as the sole fixed effect.

2.6 | Factors associated with lion movements into the Crater

We used a Poisson regression in program R to model factors associated with non-Crater-born lions entering the Crater over time. To account for differences in monitoring effort between years, we added an offset representing the log of the total number of observations recorded inside the Crater each year. We used the average annual precipitation (Abatzoglou et al., 2018) as an index for wild prey availability, where wetter years are more likely to have a higher abundance of wild prey (Ogutu et al., 2008). Resident males typically team up in coalitions, working together to prevent outside males from establishing in the area and/or becoming pride residents (Packer, 2023). Thus, the sizes of male coalitions present in the Crater likely affects the ability of immigrants to settle inside the Crater, with observations suggesting this relationship occurs on a lag (Figure 2). Therefore, we modeled the number of new male immigrants observed in a year as a function of the average size of Crater male coalitions in the previous year.

Aside from the years that conservation activities were implemented, there are additional factors which together represent the breadth of conservation activities that might foster coexistence and connectivity between the Crater and the greater NCA. These include the increased presence over time and space of Ilchokuti, represented by the number of Ilchokuti, the total number of lion observations made by Ilchokuti and the total area (km^2) surveyed by Ilchokuti each year, and the number of collared animals monitored each year as part of an early warning system to pastoralists (Figure S1, Supporting Information). Conservation activities also included prevention of lion hunts through direct intervention, however this was not included in this index given the difficulty of precise tracking due to the secretive nature of most hunts. Since all of these variables are highly correlated when measured over time, we used principal components analysis to combine them by first normalizing, centering, and scaling the data for each factor, then using the prcomp function in program R to estimate principal components. We used the first principal component representing the combined variables as a single

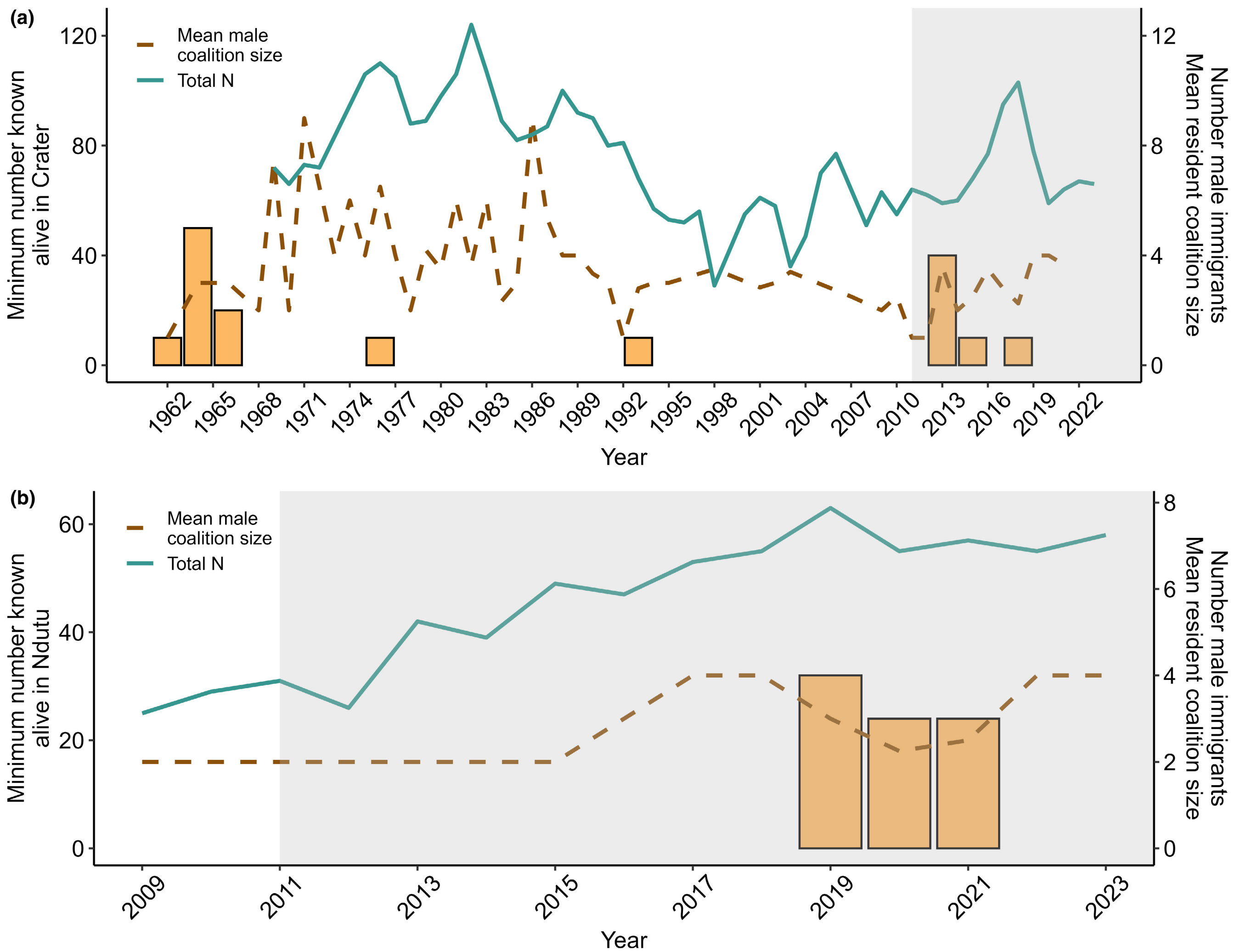

FIGURE 2 Indices of lion abundance ("Total N"), resident male coalition size and male immigrants over time for the Ngorongoro Crater from 1969 to 2023 (A) and Ndutu from 2009 to 2023 (B). Ndutu is a heterogeneous woodland and lake area on the shortgrass plains, adjacent to the Serengeti, with a higher lion density and thus considered a potential source lion subpopulation. An index of lion abundance (minimum number of unique individuals known alive) in each area (Crater and Ndutu, respectively) is shown in the blue line, the average resident male coalition size is shown in the red dashed line and the number of known male immigrants into the population is shown in the orange bars. The gray shading represents the era of conservation action for promotion of human–lion coexistence (2011–present). The lion population in the Crater increased after an initial influx of males in the early 1960s, dropping to 29 in 1998 from a peak of 124 in 1982. The population subsequently increased again following an influx of males in 2013, 2015, and 2018, the largest since the 1960s. The lion population of Ndutu also steadily increased from 2009 to 2023, with the first Crater-born males successfully dispersing to Ndutu in 2019, with further dispersers detected and establishing as resident males in 2020 and 2021.

predictor in our model to provide an index of efforts to promote coexistence within a given year.

3 | RESULTS

3.1 | Crater lion population trends, immigration, and dispersal

Since the early 1960s, the lion population of the Ngorongoro Crater has fluctuated between a minimum of 29 and maximum of 124 individuals. There have been two peaks in abundance, each preceded by an influx of multiple males from outside the Crater (Figure 2). The first major immigration of male coalitions occurred in the early 1960s after which the population climbed to its highest level in 1982 ($n = 124$; Figure 2) (Packer et al., 1991). For decades after this, there were very few immigrations (one single individual in the 1970s and another in 1990s; Figure 2) and relatively large resident male coalitions (Packer et al., 1991). The second major immigration of male coalitions occurred in 2013, 2015, and 2018, after

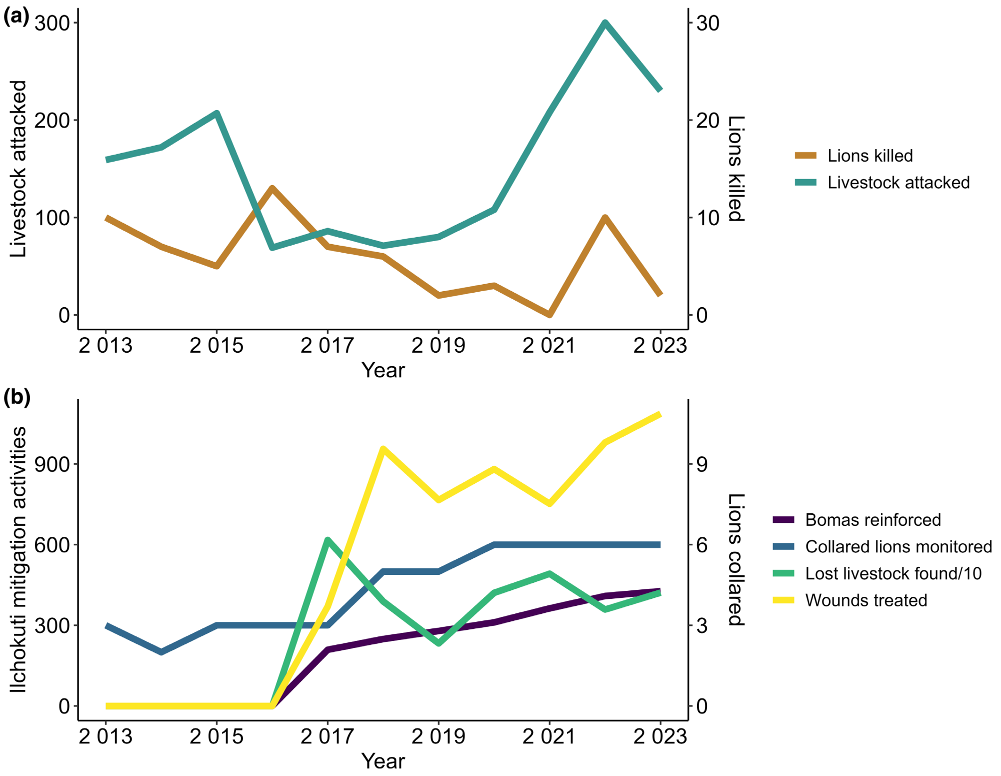

FIGURE 3 Indices of human–lion interactions and coexistence in the Ngorongoro Conservation Area, Tanzania. The number of lions killed dropped steadily from a peak of 13 in 2016 to 0 by 2021 (A), during which time Ilchokuti activities to mitigate the impacts of living with lions increased (B). In 2022, however, levels of negative interactions rose dramatically with livestock attacks and suspected lion killings increasing to the highest levels since 2012 (A), despite further increases in Ilchokuti mitigation activities (B). Several factors are likely to have increased the levels of negative interactions in 2022, including a severe drought that prompted the lions to turn to livestock due to the scarcity of wild prey, and an influx of people and livestock recently evicted from adjacent lands, thereby increasing competition over the areas' scarce resources.

conservation efforts began in the NCA in 2011 and were followed by a second peak in abundance in 2018 ($n = 103$; Figure 2). Similarly, following monitoring of the Ndutu area which began in 2009, Crater-born lions were never sighted in the area until 2019, when the first dispersal events ($n = 4$ males) from the Crater to Ndutu were noted. This was closely followed by another dispersal in 2020 ($n = 3$ males) and another in 2021 ($n = 3$ males). All of these male coalitions successfully established residency with lion prides in Ndutu.

3.2 | Promoting human–lion coexistence

While conservation activities to protect Crater lions began as early as 2011, mitigation activities by Ilchokuti to reduce negative human–lion interactions began in 2014 and mitigation efforts increased across the NCA between 2014 and 2023, as did the collaring of lions for use as an early warning system for pastoralists and to prevent retaliatory killings (Figure 3). Community engagement increased over the time of conservation activities, with additional communities requesting involvement, leading to an expansion in Ilchokuti activities (Figure S2). Increased activities to promote coexistence correlated with a decrease in the number of retaliatory lion killings from a peak of 13 in 2016 (of which five were within the REDACTED working area) to zero by 2021 despite an increase in livestock attacks by lions (Figure 3). During this time, we are aware of at least 72 lion hunts that were stopped or prevented by REDACTED intervention. In 2022, however, negative interactions increased dramatically with livestock attacks and lion killings increasing to the highest levels since 2012, despite further increases in Ilchokuti mitigation activities and efforts (Figure 3). Levels of negative interactions dropped again in 2023 with only two lions killed (Figure 3). An index of lion abundance (mean number of monthly lion observations each year collected by Ilchokuti) in the greater NCA indicates that lion use of these areas has increased significantly since 2015 (regression slope: 0.07, SE $= 0.01$, $p < .0001$), as has the area over which pastoralists are reporting lion attacks on livestock (regression slope: 0.07, SE $= 0.002$, $p < .0001$; Figure S2).

3.3 | Lion use of the NCA multi-use area

GPS tracking of individual lions beginning in 2012 indicated that most collared lions (13/25, 52%) did not move between the Crater and the greater NCA (Figure 4). This finding was supported by lion observations, where relatively few animals born in the Crater or greater NCA, respectively, left their birth area at least once (Figure 5). However, this is likely impacted by the difficulty of observing lions once they leave the Crater. Nevertheless, 19.2% (54/282) of lions born inside the Crater between 2013 and 2023 were observed at least once outside of the Crater with 3.2% ($n = 9$) being observed more frequently outside of the Crater than inside (Figure 5). When weighted by observation effort, we found a significant increase over time (between 2013 and 2023) in the probability that a Crater-born lion would leave its natal area at least once within a given year (regression slope: 5.24, SE = 0.01, $p < .0001$). This is supported by collared animals, where the average rate of movement (steps outside/total steps) away from the origin habitat (i.e., where the animal was collared; inside Crater or outside) increased significantly over time (regression slope = 2.51, SE = 0.05, $p < .0001$; Figure 6). We noted eight GPS collared males (Figures 4 and 6) moving between the Crater and the greater NCA, tending to be most active in the greater NCA during the wet season (regression slope: 1.06, SE = 0.03, $p < .00001$; Figure S3). Of those GPS-collared males, six were born outside of the Crater and moved between the Crater and the greater NCA while two were born inside the Crater and left the Crater, being predominantly active in Ndutu (Figure 4). Finally, males

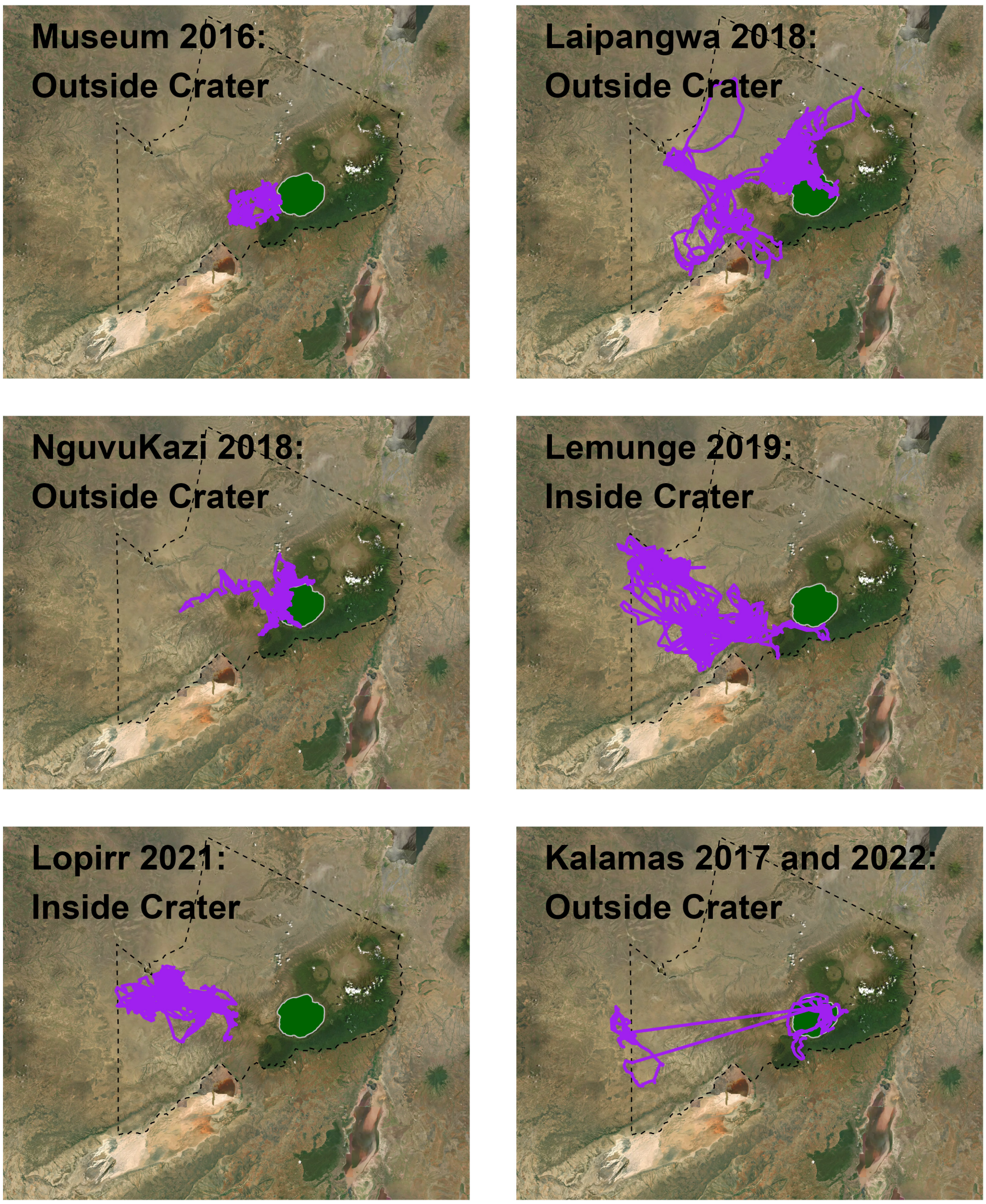

FIGURE 4 Tracks showing long distance movements of six male lions between the Ngorongoro Crater (green circle) and human-use areas of the greater Ngorongoro Conservation Area (dotted black outline), with birth locations (inside or outside of the Crater) noted. The tracks for one male, Kalamas, represent two separate collaring periods (2017 and 2022). Four males born outside of the Crater moved between the Crater and the NCA while two males born inside the Crater left the Crater and were predominantly active in the NCA.

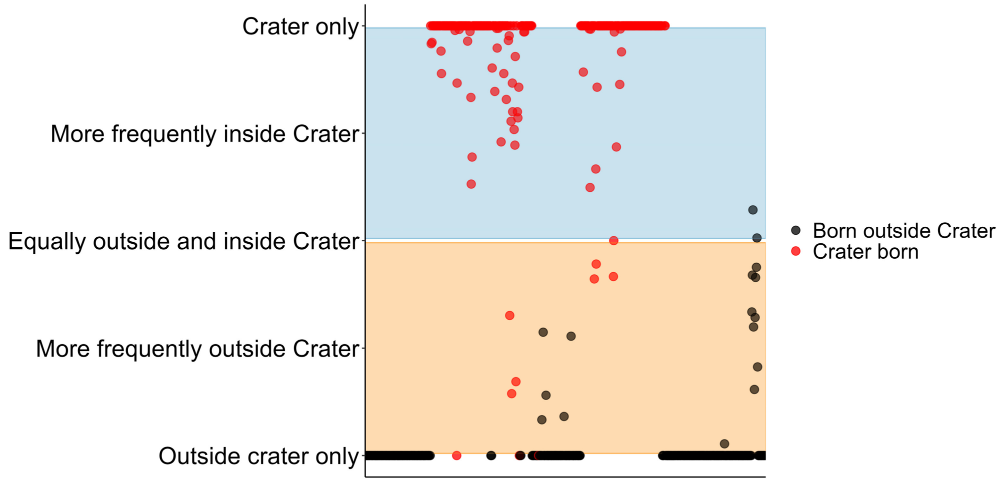

FIGURE 5 Frequency of lions that were observed solely in the Crater, solely outside of the Crater and both inside and outside, colored by birth location. Observations include 618 lions detected between 2013 and 2023. Most lions born in the Crater ($n = 282$) were only observed inside the Crater, however, 19.2% ($n = 54$) of Crater-born lions spent time outside of the Crater, including $n = 9$ lion that were sighted more frequently outside of the Crater than inside. When weighted by observation effort, we found a significant increase over time (between 2013 and 2023) in the probability that a Crater-born lion would leave its natal area at least once within a given year ($p < .0001$). By contrast, lions born outside of the Crater rarely moved into the Crater, with only $n = 6$ animals born outside the Crater occasionally entering the Crater.

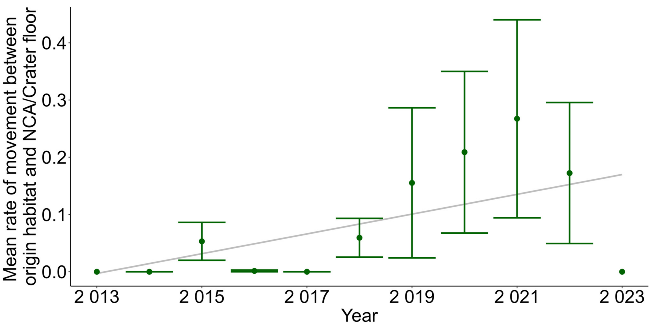

FIGURE 6 The average rate of movement (steps away/total steps) away from the origin habitat (i.e., where animal was collared; inside Crater or outside) over time, measured over 25 GPS collared lions from 2013 to 2023 in the Ngorongoro Conservation Area, Tanzania. The average rate of movement away from the origin habitat increased over time ($p < .0001$), indicating increased use of the NCA multi-use habitat separating Ndutu from the Crater.

that tended to use human occupied habitats frequently, on average, showed a significant reduction over time (regression coefficient $= -0.03$, SE $= 0.08$, $p = .0002$) in the overall area that they used in the greater NCA (i.e., the minimum convex polygon encompassing their areas of movement decreased; Figure S4).

3.4 | Factors affecting male immigration into the Crater

Our index representing conservation activities to promote human–lion coexistence was positively and significantly associated with the number of male lions moving into the Crater each year (Figure 7). Annual precipitation, a proxy for herbivore relative abundance, was also significantly positively associated with the number of male lions moving into the Crater each year (Figure 7). We found a significant negative relationship between the average male coalition size in the Crater in the previous year and the number of male lions moving into the Crater each year (Figure 7).

4 | DISCUSSION

In an world increasingly dominated by people, the conservation of small isolated populations requires fostering safe navigation across human-occupied landscapes (Dures et al., 2021). There are encouraging signs that long-distance movements (Matshisela et al., 2022) and increased tolerance (Western et al., 2019) of lions in Africa is possible with concerted conservation efforts. We evaluated whether activities to promote human–wildlife coexistence in multi-use habitats are enhancing lions' ability to exploit human-use habitats and promoting movement of lions into (and out of) the Ngorongoro Crater, Tanzania, where the human population has been steadily growing for the past several decades (IUCN, 2020). Although our study is focused on the lion side of human–lion coexistence, the human side of this equation is equally important and requires a deep understanding of the broad and complex socio-ecological system (Bauer et al., 2022; Ostrom, 2007; Redpath

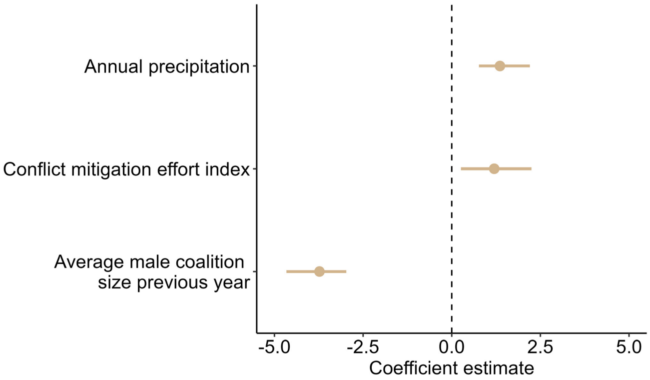

FIGURE 7 Slope coefficients associated with the number of new lions moving into the Ngorongoro Crater, Tanzania lion population each year from 1985 to 2023. Activities to promote human–lion coexistence include monitoring and outreach by Ilchokuti and GPS-collared lions to serve as an early warning system. The average male coalition size in the previous year represents males already resident in the Crater, with larger coalitions better able to prevent successful immigration (i.e., pride takeover) by outside males. Activities to promote human–lion coexistence and annual precipitation had positive relationships with the number of lions moving into the Crater each year, while average male coalition size in the Crater had a negative relationship.

et al., 2013) and measures of trust, engagement and tolerance built by conservation actions to track effectiveness (Expósito-Granados et al., 2019; Rakotonarivo et al., 2021). Anecdotally, pastoralists on the landscape indicated support and engagement with lion conservation activities, with new communities increasingly requesting inclusion in the project. Furthermore, our results indicate lion movements, dispersal success and occupancy have increased across the greater NCA, with lions increasingly able to occupy the multi-use landscape, suggesting a potential shift toward increased lion tolerance by people in the NCA. Despite our results being based on longitudinal data in a single system, without a control, the weight of these lines of evidence is compelling, indicating progress of conservation efforts toward promoting human–lion coexistence. However, increases in lion and human populations on the landscape, coupled with severe drought in 2022, have recently arrested the improvement of human–lion coexistence in the NCA, highlighting the need for continued work to mitigate negative interactions and ensure the future of the Ngorongoro lions.

Consistent with conservation activities improving connectivity for Crater lions with lions in the greater NCA, we found evidence of both increased lion immigration into the Crater and successful Crater-born lion dispersal into adjacent areas following initiation of conservation actions. Specifically, we found a positive relationship between an index representing conservation activities to promote coexistence and the number of lions moving into the Crater each year. Since the 1970s, prior to the initiation of conservation activities in 2011, immigration of lions into the Crater was rarely observed. Following the commencement of conservation actions, "new," unknown, males joined the Crater population in 2013, 2015, and 2018 and there followed a "cub boom" which almost doubled the Crater population size. Genetic analyses underway will reveal if these males injected new genetic material into the population (Jansson, 2024); nevertheless, their presence alone is encouraging. At the same time, we noted a significant increase in the movement of lions away from their natal area (i.e., from the Crater to greater NCA and vice versa) over the years of conservation action (2013–2023), consistent with connectivity between the Crater population and the greater NCA improving, with exchanges being facilitated in both directions. This is good news for the Crater lion population given its history of isolation and inbreeding (Jansson et al., 2024; Packer, 2023; Packer et al., 1991) and provides evidence that conservation efforts can successfully provide connectivity between the Crater population with the larger Serengeti lion population. Indeed, following 10 years of monitoring in Ndutu without Crater-born immigrants being detected, the first successful Crater-born males arrived in Ndutu in 2019 and those movements have continued, indicating improvement in lion ability to safely cross the multi-use area.

While enhancing the ability of lions to cross multi-use areas safely to maintain connectivity between the NCA and greater Serengeti ecosystem is the primary goal of our conservation efforts, the ability of lions to settle in and successfully exploit multi-use habitats is an important indicator of success in fostering human–lion coexistence. After 2011 and as conservation efforts in the NCA increased thereafter, we noted increases in the foray lengths of collared male lions into the greater NCA. Furthermore, we made the first known observations of Crater lions settling in the multi-use area, later joined by nomadic males of which some were born outside of the Crater. Precipitation appears to enhance the ability of lions to occupy and move through the greater NCA, possibly because human activity tends to be less intense across the landscape during the times of greater wild prey abundance in the wet season and in the wettest years (Ikanda & Packer, 2008; Jansson et al., 2024). By contrast, the presence of large male coalitions in the Crater appears to discourage new immigrants, likely a function of larger resident coalitions being able to easily chase off solitary immigrants or smaller immigrant coalitions (Packer, 2023). Indeed, a large male coalition that became resident in Ndutu in 2021 likely prevented new immigrants from settling there in 2022 or 2023. Despite large male coalitions dominating the Crater floor, we have observed several instances of dispersing males consorting with females by entering the Crater for brief periods without establishing residency, or consorting with Crater females just outside the Crater. We have also observed NCA males teaming up with Crater-born nomads to enhance their coalition size, thereby improving potential breeding success. While it is unclear whether these strategies result in new genetic material entering the Crater, it is evident that they rely on lion survival in the greater NCA for success.

Retaliatory and ritual killings have likely been major factors preventing successful movements of lion through and occupation of multi-use areas. While our counts of lion killings represent only a minimum known and/or suspected number, lion killings dropped steadily from 2011 to 2021, despite more lions in the area and an apparent expansion of the area over which negative interactions occur. This putative success has been possible through a combination of a reduction in lion-livestock attacks (e.g., early warning systems of lions in the area, boma reinforcement, retrieving lost livestock), reduction of livestock mortality following attacks (e.g., wound treatment), keeping the lions safer by preventing hunts and directly stopping lion killing, and reaching agreements with the communities to abstain from killing lions. This suggests an ability to increase human tolerance of lions in the region, even in the face of steadily increasing human populations, which is supported by the settlement of lions in multi-use habitats of the greater NCA.

However, despite efforts to promote coexistence, greater numbers of lions on the landscape have led to an increase in livestock attacks. After 9 years of decline, the level of negative interactions rose sharply in 2022 with at least a suspected 10 lions killed and 162 reported lion-livestock attacks (comprising 219 livestock killed, 71 injured)—a 35% increase from the previous year despite continued increases in efforts to promote coexistence. The heightened level of negative interactions in 2022 is attributable to a number of factors, including greater lion presence in human-occupied areas, severe drought which limited resources for both lions and people, and an influx of new people and livestock into the NCA following evictions from an adjacent area (i.e., Pololeti, a section of Loliondo, including its important water source at Oseru). Although levels of negative interactions dropped again in 2023 with only two lions killed and a 23% decrease in lions attacks on livestock, the spike in 2022 highlights the unpredictable nature of the conservation landscape, where environmental, ecological, and socio-economic factors can change rapidly, impacting the efficacy of conservation activities. Furthermore, conservation success which facilitates lions occupying a multi-use landscape may reach a social carrying capacity, where tolerance fades at elevated levels of negative interactions (Breitenmoser et al., 2005). While effective promotion of human–lion coexistence appears achievable, the need for mitigation of negative interactions and community outreach may continually increase, requiring conservationists to be nimble and resolute to adequately meet the demands of highly dynamic socio-ecological conditions.

Living among wildlife, especially large carnivores, can impose a significant financial burden and often the local people shouldering that burden do not receive the financial benefits of wildlife conservation (i.e., tourism dollars). Taking an inclusive approach to conservation is key to making sure the burden of living with wildlife is being alleviated, which fosters tolerance and promotes coexistence (Young et al., 2021). Approaches that further decrease the costs of living with carnivores can increase the ceiling of social carrying capacity beyond baseline levels (Pekor et al., 2019), enhancing conservation success. For example, REDACTED is piloting Conservation Incentive Payments (CIP) in six villages of the NCA, where communities earn monetary incentives for allowing lions to occupy and safely pass through community lands. While further evaluation of the success of this program and others like it is warranted, early indications are encouraging (Jansson, 2024) and could provide a vital strategy for inclusive conservation, especially with large carnivores. Thus, the prospects for the future of human–lion coexistence in the NCA look hopeful, however, success requires continued flexible, creative, and determined conservation efforts that engage and earn the support of local communities.

Our results are encouraging for conservation efforts in similar landscapes where lions and humans co-occur (e.g., pastoralist landscapes in Northern Tanzania, and Southern Kenya); however, success hinges upon trust-building, requiring engagement and collaboration with local communities and a long-term commitment by conservationists (Hazzah et al., 2019). We also note that the coexistence landscape of the NCA is perhaps less complex than other nearby ecosystems as only traditional pastoralism is permitted in the NCA with fewer conflicting land-use interests such as agriculture, which may increase the challenges involved in promoting human–lion coexistence (e.g., the nearby Tarangire Ecosystem) (Kissui et al., 2022). As countries around the world re-commit to a future where people live in harmony with nature (Joly, 2023), the successes and lessons learned from the NCA provide encouraging signs for inclusive conservation, and avenues for further work, in coexistence landscapes where the persistence of large carnivores lies in the balance.

ACKNOWLEDGMENTS

This research was carried out under permissions granted by the Tanzania Commission for Science and Technology (COSTECH) and Tanzania Wildlife Research Institute (TAWIRI). We acknowledge the Government of Tanzania, TAWIRI, and especially the Ngorongoro Conservation Area Authority for support and collaboration. We thank the Lion Guardians for all support, advice, and inspiration to get KopeLion up and running. We would like to thank L. Foley for scientific advice on the study. This work would not have been possible without the KopeLion team, support from local stakeholders, in particular the Ndutu Safari Lodge and Masek lodge. In particular, we thank the NCA communities for their engagement and commitment to coexistence.

DATA AVAILABILITY STATEMENT

Data are available from Data Dryad: https://datadryad.org/stash/share/15pFiW0ckGqepDX3hkdfipBjTDPkm-r_oDpOsZkXv6Y.

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SUPPORTING INFORMATION

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

How to cite this article: Parsons, A. W., Sandström, C., Capper, S., Faust, L., Kissui, B. M., Packer, C., & Jansson, I. (2025). The benefits of inclusive conservation for connectivity of lions across the Ngorongoro Conservation Area, Tanzania. *Conservation Science and Practice*, *7*(3), e70001. https://doi.org/10.1111/csp2.70001