# The Complex Landscape of Lion Behavioural Ecology & Conservation: from Social Dynamics to Systemic Inequality

**Lauren F. Rudd**

Green Templeton College and the Department of Biology
University of Oxford

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*“Little bubbles of air snapped as these voiceless animals of the earth came to the surface […]. I don’t know why, but this seemed like one of the nicest things I had learned in the woods- that earthworms, lowly, confined to the darkness of the earth, could make just a little stir in the world.”*

From *My Side of the Mountain*,
by Jean Craighead George

# Abstract

The African lion *(Panthera leo)* is a globally significant species due to its cultural, financial, and ecological status. Unique amongst *Felidae,* lions are highly social and group-living which contributes to their charisma. Despite their status, the species faces significant conservation pressures. Many of these threats, such as human-lion conflict and prey-base depletion, are influenced by the sociocultural landscapes within which lions' range. Even natural threats such as disease are exaggerated in severity and spread by anthropogenically induced climate change and contact with domestic animals.

In this thesis I take a holistic view of lion conservation, combining methodologies from behavioural ecology and social science, to address knowledge gaps within the complex system of lion conservation. I evidence sex-specific patterns of social ageing in the African lion. In females, I highlight the role of associate loss and within-individual shifts in sociality prior to disappearance in driving social ageing patterns. Further, I show that individual-level sociality impacts longevity across both sexes. These findings have consequences for disease transmission and species management strategies across age-structured lion societies. Next, I evidence identity-bias against lion conservation messengers on social media based on their expertise, race, and gender. I demonstrate that racism and sexism influence messengers' perceived credibility in the public eye, and support for their conservation recommendations. Finally, I trace conservations' colonial history into present-day dynamics to better understand why such discrimination exists - before suggesting ways to create a more socially just and inclusive sphere of conservation.

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# Author contributions

All work presented in this thesis is primarily my own.

This thesis is presented as a collection of independent research chapters, each in scientific journal format, with an additional thesis introduction and discussion. I am lead author of each research chapter, and sole author of the introduction and discussion. As of the date of thesis submission, **Chapter 2** has been accepted for publication in *Current Biology*, **Chapter 4** is in review in *Conservation Biology,* and **Chapter 5** is published in *Proceedings of the Royal Society B: Biological Sciences.* Below I list the author contributions for each research chapter in turn.

### Chapter 2

Craig Packer provided the data used. Dora Biro, Craig Packer, Josh Firth and Greg Albery helped to conceptualise the research and provided input on manuscript draft revisions. Gregory Albery helped to conceive the methodologies used and conduct the formal analysis.

### Chapter 3

Craig Packer provided the data used. Dora Biro, Craig Packer, Josh Firth and Greg Albery helped to conceptualise the research and provided input on draft revisions. Greg Albery helped to conceive the methodologies used and to conduct the formal analysis.

### Chapter 4

Shorna Allred, Amy Dickman, Darragh Hare, and Yolanda Mutinhima helped to conceptualise the research. Darragh Hare helped to conceive the methodologies used and to conduct the formal analysis. All co-authors provided input on manuscript draft revisions, as did Dora Biro.

### Chapter 5

Julius G. Bright-Ross, Andrea Davalos, Darragh Hare, Merlyn Nomusa Nkomo, Tanesha Allen, Amy Dickman, and Moreangels M. Mbizah helped to conceive of the idea. In addition to these co-authors, Shorna Allred, Kartik Shanker, Duan Biggs, Michael Dunaway, Ritwick Ghosh, Nicole Thompson Gonzalez, Thembela Kepe, Sara L. Middleton, Meera Anna Oommen, Kumar Paudel, Claudio Sillero-Zubiri provided comments on the manuscript drafts.

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# 1. General Introduction

## 1.1. Thesis aim and objectives

The overall aim of this thesis is to improve interdisciplinary knowledge of African lion *(Panthera leo)* behaviour and conservation. In a rare approach, I bring together methodologies traditionally associated with either behavioural ecology or conservation science to address key gaps in our knowledge. As such, this thesis was heavily shaped by the broad spectrum of research approaches I was exposed to on the interdisciplinary Environmental Research Doctoral Training Program. First, I explore aspects of lion sociality related to ageing and inter-individual relations that have previously been overlooked due to data limitations and an absence of appropriate analytical frameworks. Second, I interrogate the ways in which decision-making based on such findings could be influenced by inter-personal dynamics within the wider lion conservation community, including the public sphere. Specifically, I highlight the role of conservations' colonial history in reinforcing ongoing injustices. I focus on the following main objectives:

i. To utilise novel spatial-social network methodologies to better understand individual-level variation in African lion social behaviour

ii. To explore the consequences of social ageing and the social dynamics of individual loss on an African lion population, with a view to informing future species management

iii. To explore understudied aspects of science communication, by quantifying the impact of identity-bias on public perceptions of lion conservation messengers

iv. To provide societal context for the thesis as a whole, by examining how colonial histories contribute to ongoing racism in conservation science and practice

## 1.2. Thesis Layout

This thesis is comprised of 6 chapters. The current chapter provides a short background to the researcher (Section 1.3. below), followed by an introductory review of the literature relevant to the research chapters. The main research contributions are presented in **Chapters 2-5**, each written as an independent and self-contained manuscript, with further details below. **Chapter 6** provides a general discussion of the main findings from each research chapter in tandem, alongside a consideration of the research limitations and fruitful directions for future work.

**Chapter 2** applies novel spatial-social network analyses to the long-term dataset of the wild Serengeti African lion population to investigate sex-specific social ageing patterns and the impacts of lifetime sociality on longevity.

**This work is published as “Sex-specific social ageing in wild African lions” in Current Biology (Rudd et al., 2024).*

**Chapter 3** examines pre-disappearance changes in social behaviour, and the social impact of associate loss on African lions, using the previously established spatial-social network analyses (following **Chapter 2).**

** This work is in the manuscript preparation phase.*

**Chapter 4** investigates bias in public perceptions of lion conservation messengers on X (formally Twitter), using a novel vignette-based experimental method. I focus on identity-bias along the axes of race, gender, nationality, and expertise.

**This work is in review as “How identity-bias influences public perceptions of conservation messengers on social media” in Conservation Biology (revised and resubmitted, January 2025).*

**Chapter 5** outlines the past and present patterns of racism in conservation practice and science, and makes recommendations for building a more equitable future for conservation.

**This work is published as "Overcoming racism in the twin spheres of conservation science and practice" in Proceedings of the Royal Society B (Rudd et al., 2021).*

## 1.3. Positionality Statement

To reflect the increasingly interdisciplinary nature of conservation and behavioural ecology research, there have been growing calls for researchers to issue statements of positionality[1,2]. Such reflective statements allow identification of potential biases the researcher possesses that could influence the framing of their work. Subsequently, the potential for positionality statements to cause harm[3] and replicate colonial research practices[4] have been identified. As such, there is no consensus on best practice regarding positionality statements. Below I briefly reflect on my individual, sociocultural and geographic positionality as relevant in my approach to the research and data within this thesis.

The motivation for this thesis was born out of a desire to combine my interests in applying animal behaviour (particularly social behaviour) to species conservation, my passion for social justice, and my commitment to diversifying perspectives in academia. Most of my undergraduate studies at The University of Edinburgh followed traditionally “western” theoretical frameworks in biology. However, an exchange year at the University of Queensland in Brisbane opened my eyes to broader ways of learning, particularly in relation to Indigenous Knowledge (IK) systems and field-based practical learning. The exchange year also allowed me to take modules in non-core areas, such as international development, media studies, and science communication. I believe this stoked a curiosity about the intersections of broader societal issues within ecology and conservation that would later be pivotal to my DPhil research.

I am a sociocultural, economic, and geographic “outsider” of the Mara and Simiyu Regions of Tanzania where The Serengeti National Park is, and where the data used in **Chapters 2 and 3** of this thesis were collected. The decision to work with the Serengeti Lion Project data for my DPhil thesis research was borne out of prior difficulties with field data collection, which were worsened by the global covid-19 pandemic. The travel restrictions imposed by doing DPhil research during this time, combined with the sunk financial costs of work prior to the pandemic, further prohibited me from visiting the Serengeti myself. As such, I have relied heavily on contextual information generously shared with me about the data and Serengeti system by those who collected it. However, I am acutely aware that none of the people I have communicated with regarding the data are themselves locals to the system, or Tanzanian. As such, I have made a concerted effort to enhance my knowledge of the social and ecological landscape of the Serengeti (and neighbouring regions) by engaging with educational material from a broad diversity of sources. I have also been careful to refrain from conducting research that would have tangible or immediate implications for policy in the Serengeti, and instead focused on laying the groundwork for future research to address the gaps I identified.

## 1.4. Background and literature review

### 1.4.1. Social systems and structure- a network approach

Animal social systems are inherently complex in nature, as they are governed by both external environmental variables, and internal species characteristics[5,6]. There are several inter-related components of social systems. *Social organisation* is the most foundational and describes the size and cohesion of units in the system, with similarity expected across all populations of a particular species[7]. The *mating system* is a related but distinct component, encompassing both the quantity of mating partners and frequency of mating interactions[8]. Finally, the *social structure* describes the social interactions, and so the relationships, between individuals within the system which are in constant flux[9]. The dynamics of these interactions are dependent on the demographic characteristics and social behaviour of each interacting individual[10]. As such, interactions may vary based on the integral characteristics of each individual (e.g., their sex or dominance rank), their genetic relation to one another, and the individuals' adaptive social behaviour which can be influenced by the wider environmental or social conditions[6]. In this way, not only do the nature of the interactions between individuals build the social structure of a system, but the social structure itself also influences the pattern of interactions occurring within it.

Studying the nature of social interactions between individuals historically depended on examinations of dyadic relationships or group-level structure in isolation. The suggestion to apply social network theory to animal systems dates back to 1975[11], though its uptake was initially limited to descriptive studies due to the frameworks' high data and computational demands[12–15]. A social networks approach has a multitude of benefits, primarily in the ability it confers to examine individual, dyadic, group, and population level sociality patterns within the same framework[16]. Social networks can be broken down into two main components. The "nodes" classically represent the individuals within the population of interest and their phenotypic attributes (though they can be used to represent groups of individuals, see[17]), while the "edges" represent the interactions between them. In this way interactions between nodes can be modelled as a network, and metrics can be mathematically calculated to describe its resultant social characteristics in different ways[18].

The flexibility of a social network approach allows interactions between individuals to be modelled in the most suitable manner for the question at hand. Defining the relationship the edges represent is within the researcher's control, but most commonly in animal behaviour, they reflect the co-occurrence of individuals (Fig. 1A). Networks constructed in this way facilitate an understanding of the inter-connectedness of individuals in a population and can be used to ask a vast array of biological questions[19]- for example about the spread of disease[20–22] or information[23–25]. Such edges can further be "weighted" by the proportional frequency of interactions between individuals (Fig. 1B). The collection of more detailed interaction data, such as inter-individual affiliative interactions (e.g., grooming behaviour), or agonistic interactions (e.g., fighting behaviour) allows context-specific network construction[19]. Capturing such behavioural interactions further facilitates the edges to be modelled in a directional manner (Fig. 1C). In this way more nuanced questions can be asked; for example, whether correlations exist between the directionality of grooming behaviour, aggressive behaviour, and dominance rank[26].

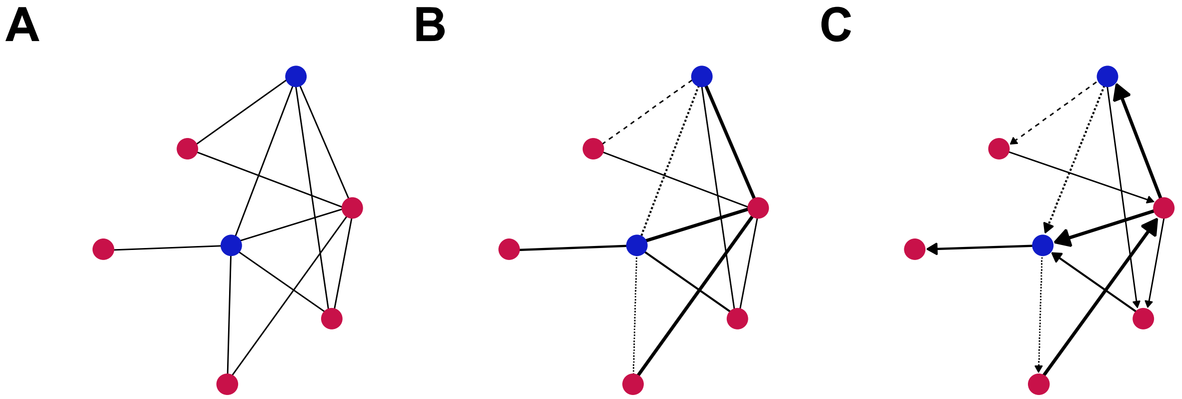


**Figure 1. Methods of social network construction.** Multiple ways of constructing social networks are illustrated, with increasing levels of detail from left to right. In this example, the nodes are coloured to indicate individual sex (red = female, blue = male). In A, individuals are connected via uniform edges, which indicate co-occurrence in space and time. In B, the relative frequency of co-occurrence in space and time between each of the individuals is conveyed via the thickness of the edge, with thicker lines representing stronger connections. In C, the ability to construct a network using more detailed interaction data is shown. Arrows denote the direction of an interactive behaviour, (e.g., grooming), hence the network shows the relative frequency and directionality of an affiliative behaviour between individuals.

While static social networks capture the social structure of an animal system within a given time frame (e.g., by incorporating the social interactions of interest over a 1-year period), temporal network analyses facilitate the understanding of dynamic changes to the social structure through time[27]. There are two conventional ways of conducting temporal network analyses. The first, known as time-ordered networks, involves modelling edges that each have a specific start and end time. Networks made in this way can be useful for examining ordered interactions within a system, therefore allowing the precise flow of a socially transmitted entity (e.g., information) to be traced[28]. Alternatively, time-aggregated networks are constructed in the same way as static networks, but a unique network is built for each time-step of interest[27] (Fig. 2). For example, cooccurrence networks could be built at yearly intervals over a five-year period, and each of the five networks would encompass all recorded interactions within a given year. This facilitates changes in individual network metrics, and changes to the overall network structure, to be traced and quantified through time (see [29–31] for examples).

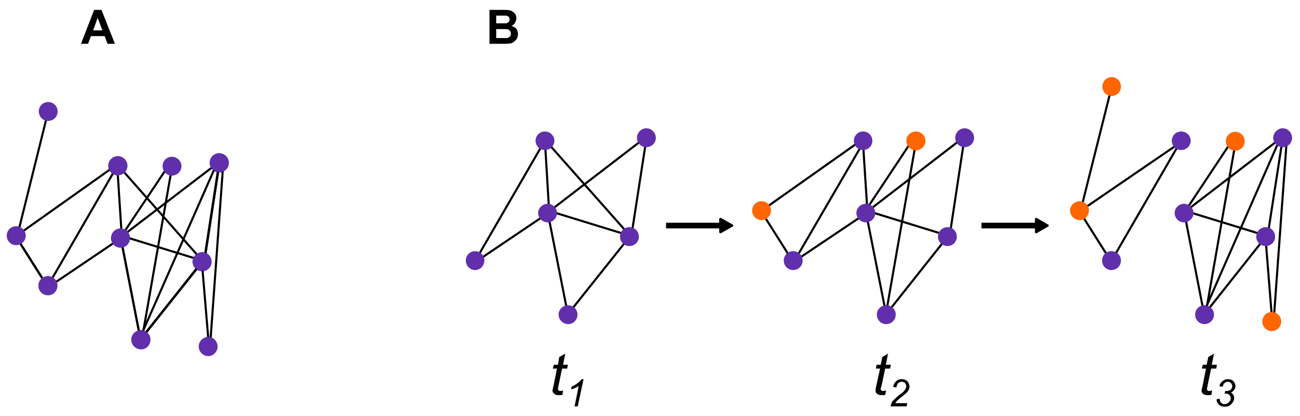


**Figure 2. Static versus time-aggregated social network construction.** Comparing the static network (A) with the time-aggregated network series (B) illustrates the value of considering temporal shifts in sociality. In this example, time-aggregated networks ($t_1$, $t_2$, $t_3$) show all interactions occurring within that time period. The static network shows all interactions over the three time periods combined. In the time-aggregated network series, it is possible to identify individuals that enter the system after $t_1$ (nodes coloured orange) and trace the resultant fragmentation of the population.

It is increasingly recognised that not only does time influence the sociality of individuals (and so systems), but so too does space. Spatial and social behaviours are frequently driven by similar underlying mechanisms, including fundamental processes such as mating and foraging[32,33]. Individuals' spatial and social behaviours further impact one another in a multitude of ways. For example, an individuals' social environment can influence spatial behaviours such as dispersal[34–36] or home range size[37], while the spatial distribution of resources may drive social interaction patterns of both a competitive and cooperative nature[38]. Despite this, studies that specifically target the spatial-social interface are limited[39]. Recent advances in social network methodologies – the fitting of stochastic partial differential equations (SPDE) within the integrated nested Laplace approximation (INLA) R package - have facilitated investigations of social interaction patterns that account for the potential confounding effects of spatial behaviour. The importance of this approach has been demonstrated across ungulates[40,41], birds[42] and carnivores[43].

### 1.4.2. Individual variation in sociality

Social network analyses are particularly useful in exploring individual-level variation in social behaviour and association patterns within a social system. Given the high flexibility and adaptability of behaviour, it follows that extensive variation in sociality would exist between individuals, social groups, and populations of the same species[6]. Such variation can be influenced by a suite of factors, including those intrinsic to the individuals interacting, and their environmental context (both social and ecological)[10,44,45].

Sex-based differences in sociality are likely to follow the constraints imposed by a species' mating system. For example, the social organisation imposed by monogamous systems compared to polygamous systems will impact the availability of conspecifics in a sex-dependent manner, and the frequency of interactions amongst them[46]. The partition of parental or alloparental care may also influence associations across the sexes[47], as will intra-sex and inter-sex cooperative and competitive dynamics (e.g., over access to mates or resources)[48]. Social network analyses have evidenced such sex-based individual differences in social interaction patterns across taxa and species including primates[49,50], cetaceans[51], and lizards[52]. Other aspects of life history, such as dispersal, frequently differ between the sexes and have strong impacts on an individuals' social partners and interaction patterns[53–55]. Similarly, and with such life history events in mind, the age class of an individual can further impact their relationships, as has been shown across several mammalian species[56–59].

Beyond variation between age classes, understanding shifts in sociality within individuals as they age (commonly referred to as "social ageing") is a growing area of research within the broader study of senescence in wild animal populations[60]. Traditionally ageing studies in animals have focused on declines in physical condition[61] and reproductive success[62–64], both of which could interact with changes in sociality. Studies have also described the potential implications of senescence, such as reductions in foraging performance[65,66] and immune system strength[67–69], which could again impact sociality[67,70]. Changes in sociality with age could infer a broad range of consequences for not only the focal individual, but also the structure and organisation of the entire social system[71]. Several non-exclusive hypotheses have been suggested to predict social ageing, broadly categorised as either within-individual changes (e.g., competition avoidance, social exclusion, and spatial behaviour changes), or population-level changes (e.g., selective disappearance or demographic shifts in population composition)[40,72].

One example of social ageing can be found in female red deer (*Cervus elaphus*), which have been shown to alter their social and spatial behaviour in tandem. Declines in social connectedness were evident as individuals aged, coupled with declines in home range size and a preference for areas that were less central, less densely populated, and contained lower-quality grazing[40]. Female rhesus macaques (*Macaca mulatta*) were also found to have smaller social networks with age. These declines were driven by ageing females' increased selectivity of partners; specifically for kin and those who they were strongly connected to in early life. Such shifts existed despite individuals spending a similar overall amount of time engaging in social interactions[73]. As such, current knowledge from mammalian systems indicates a strong role of within-individual changes in driving social ageing. However, research is needed across more varied social systems to determine the extent to which patterns of social ageing are consistent throughout animal societies, and to further elucidate its potential causes and consequences.

The existence of within-individual changes in sociality with age can be considered within the broader context of social behaviour shifts and individual loss from a population. While age-driven mortality is one cause of loss, demographic processes such as dispersal, eviction, and population splintering can similarly affect the social structure of a system[10]. In the two years prior to a mass eviction event, female rhesus macaques that would be evicted displayed noticeable changes in their social partner choice and became collectively more cliquish, engaging in fewer affiliative interactions with others[74]. Moreover, mass eviction events in the banded mongoose (*Mungos mungo*) have been found to reduce intra-group reproductive competition, but increase inter-group conflict, with implications for the structure of the population[75]. The extent and centralisation of agonistic interactions in yellow-bellied marmot (*Marmota flaviventer*) social systems has further been found to impact dispersal decisions[76].

Perturbation events, both acute and long-term, also impact individual behaviour and the wider social system within which they exist. In wild house mice (*Mus musculus domesticus*), a dramatic decline in population numbers caused by the introduction of a predator did not impact group-level population structure. Instead, individuals were differentially impacted based on their prior sociality; highly social individuals reduced their number of social partners, while less social individual gained new associates[77]. Rhesus macaques responded in a similar manner to a mass mortality event (Hurricane Maria, 2017), in that previously isolated individuals increased their affiliative social connections and gained additional associates, rather than strengthening relationships with existing ones[78]. Furthermore, the social structure of an African elephant (*Loxodonta africana*) population was somewhat resilient to individual loss, with daughters assuming similar social network positions to their mothers during periods of increased mortality due to poaching[79].

Experimentally induced disturbances through the targeted physical or simulated removal of individuals from a system have shown similar results in birds and mammals. In wild great tits (*Parus major*), there was a positive correlation between individuals' prior association strength to a removed individual, and subsequent increases in the quantity and strength of their social connections, and their overall connectedness within the network[80]. Comparable findings were apparent following a cull of Canada geese (*Branta canadensis*); surviving individuals gained new associates to compensate for those lost, while also strengthening their existing relationships[81]. At a systems level, killer whale (*Orcinus orca*) populations have been suggested to be vulnerable to becoming socially fractured into small clusters following the computationally-simulated loss of key individuals, such as juvenile females and those from specific matrilines[82]. Additionally, individuals were found to have a reduced number of associates and be less strongly bonded to them during a period of high mortality. After this disturbance, individuals increased their associations with individuals from other groups (thereby replacing their lost associates) but the stability and strength of their new relationships were low[83]. Combined, the findings from these studies of the drivers and consequences of individual loss have illuminated the interplay between sociality, demography, and disturbance. However, our knowledge is still limited in comparison to the vast diversity of animal social systems and species, and does not extend to the social dynamics of natural, ongoing, individual turnover in stable populations.

The increasing focus on the social dynamics of ageing and individual loss reflects an understanding of their potential ecological consequences. Social learning is an important mechanism through which individuals can adapt to their environment, especially under frequently changing or risky conditions. As individuals are likely to continually build knowledge with age[84,85], shifts in the sociality of ageing individuals may have repercussions for information spread through populations[86]. Age-related changes in social connectivity could further interact with immunosenescence and disease resistance to influence the likelihood of pathogen exposure and susceptibility[67,70]. This will be particularly key to investigate in flexible, fission-fusion systems where contact rates between individuals are varied, and especially in species known to be at risk of lethal disease outbreaks. Furthermore, examining the impacts of individual loss is important in understanding the ability of populations to respond socially to increased disturbance regimes under increasing climatic and anthropogenic pressures[45], and the fine-scale effects this may have on individuals.

As outlined, individuals display high degrees of variation in their social behaviour, social strategy, and social network position. This is important given that being socially well connected has been found to correlate positively with fitness and survival in several species[87], making fine-scale sociality a priority area of study for social species of conservation concern. There are two leading hypotheses which have been formulated to explain this phenomenon. The “main effects” hypothesis proposes that social associates, and relationships in general, provide direct emotional and behavioural support to encourage healthy behaviours[88]. Evidence to support this hypothesis is primarily linked to human societies[89,90]. The “social buffering” hypothesis is more commonly considered in studies of animal sociality. It suggests that social connectivity offers protections against stressors and aversive experiences that would ordinarily have a negative impact on survival[91]. Evidence of the benefits inferred by social connectivity to individual health and longevity are numerous in primates[92–97], and have additionally been found in cetaceans[98] and ungulates[99]. Increasing our knowledge of species in which the nature of social interactions and the population social structure can impact individual fitness may aid in highlighting the mechanisms responsible. The unique ecological and evolutionary dynamics of social carnivores make them ideal study systems for such research, and for studying processes related to association patterns such as social ageing and the dynamics of individual loss.

### 1.4.3. The Serengeti lions as a study system

One such social carnivore species that is ideal for the study of fine-scale social dynamics is the African lion (*Panthera leo*), unique amongst felids for living in egalitarian, fission-fusion social groups. Specifically, the lion population inhabiting the Serengeti National Park, Tanzania, is a candidate system due to its long-term monitoring by the Serengeti Lion Project[100]. Research on the Serengeti lion population began in the 1960s, though the consistency and frequency of data collection was highest between 1984 and 2014 when GPS collars were fitted on at least one female per pride. Since then, extensive data on the spatial and temporal cooccurrence of known individuals has been collected (defined as being within 200m of each other, and recognised by facial markings), alongside individual-level demographic data, such as sex and age. This data was used to construct the annual social networks (across the 30-year study period) for the analyses conducted in **Chapters 2 & 3** of this thesis.

The studied population inhabits a 2700km$^2$ area, approximately in the centre of the park (on a north-south axis), which consists of an open grasslands (plains) habitat, and a more densely vegetated woodlands habitat[100]. There are two broad seasons: the dry season spans June to October, and the wet season spans November to May[101]. Seasonal rainfall patterns drive large annual migrations of prey species including wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and Thomson's gazelle (*Eudorcas thomsoni*) through the study area, with rainfall and prey densities higher in the woodlands habitat year-round. Predators, including lions, track these prey movements meaning their home range territories shift geographically across the year[102,103]. These famous annual migration patterns across the Serengeti landscape are considered one of the greatest wildlife tourism spectacles in the world[104].

Owing to the long-term study of the Serengeti lion population, its social organisation and mating system are relatively well understood. Related adult females and their cubs form prides that collectively hunt, defend a territory, and rear young[105]. These prides can range in size from 2-20 individuals, but frequently splinter into smaller sub-groups, and individuals commonly spend time alone. The composition of these sub-groups fluctuates daily, and pride-mates remain within a 5-6km radius of each other, likely to maximise communication efficiency (via roaring)[100]. The majority of female offspring (~75%) are recruited into the mother's pride, but dispersal does occur, particularly when the optimum pride size would otherwise be exceeded. Daughters that disperse do so in cohorts of sisters and cousins after the age of 2 years, forming new prides with territories adjacent to their mother's[100,106,107]. Conversely all male offspring disperse in cohorts of brothers and cousins between the ages of 2 to 4 years. They enter a nomadic life stage, and during this time can form alliances with other nomads, leading to the formation of male coalitions of up to nine individuals. These coalitions eventually outcompete a resident coalition to take over a pride (or two neighbouring prides) of females, usually once the males have matured and reached adult body size[100,107–109]. Incoming males are infanticidal, and pride takeovers can therefore trigger early dispersal of sub-adults and the splintering of prides. Once a coalition has residence of a pride the membership of the coalition remains constant, barring the occasional and rare recruitment of sons[100].

There is no clear dominance hierarchy, meaning female pride mates and male coalition mates display similar reproductive rates[64,110]. However, there is considerable variation in the per capita reproductive success between prides. This can be attributed in part to territory quality and in part to pride size, with greatest reproductive success experienced by females in mid-sized prides[106,111]. Females creche their cubs to share the caring and nursing responsibilities, facilitating continued engagement in group and solitary hunting for mothers[105,112]. Reproductive senescence begins at ~ 10 years old, with both cub survival and litter size declining[64]. There are no obvious benefits of grandmothers to the survival of their grand offspring, unless they are actively breeding themselves and so sharing care of the creche[100]. Outside of reproduction, lions engage in a suite of cooperative group behaviours including hunting and territory defence[105,113–115]. While studies have focused on explaining why lions are social, little is known about inter-individual interaction patterns and individual-level variation in sociality.

Understanding fine-scale social structure in this population may aid in its future conservation management. The Serengeti lion population has historically suffered high levels of mortality because of severe and cyclical disease outbreaks- predominantly canine distemper virus (CDV)[116–118]. Such outbreaks are worsened by climate extremes[119] and may be fuelled by inter-species interactions[120], with domestic dogs a potential reservoir[121,122], meaning future management of disease dynamics is a key concern for this species. More broadly, the African lion faces significant threats in addition to disease and climate change across its range (e.g., prey depletion, habitat loss, and human conflict)[123], the management of which may be aided by deepening our understanding of individual sociality[124]. In the previous section (1.4.2) the value of a social networks approach in understanding the social dynamics of perturbations and individual loss from a system were examined. Such an approach is particularly relevant and pertinent to lions, given their complex sociality and increasing conservation concern.

### 1.4.4. Colonialism in lion conservation

Due to rapid rates of population decline, the African lion is classified as vulnerable and decreasing on the IUCN red list[125]. Threat analysis has determined that human-lion conflict (the retaliatory killing of lions due to the real and perceived threat they pose to human lives and livelihoods) and prey depletion (via bushmeat hunting) are the greatest threats in terms of the number of lions, and lion populations, they threaten. Additional pressures exist due to the expansion of cropland and livestock grazing areas, the increasing isolation and vulnerability of small populations, unsustainable forms of trophy hunting, and resource extraction[123]. Given many of these factors are rooted in the socio-economic landscapes within which lions range, a holistic approach to lion conservation is needed. Studies have increasingly sought to understand the attitudes of local communities towards lions and examine factors that might influence perceptions in such a way that conflict behaviours can be changed[126–129]. Efforts to reduce livestock depredation and retaliatory killings have seen some success when communities are properly engaged[130,131]. Financially compensating farmers when livestock are killed can also be effective, though it can simultaneously create unsustainable financial dependencies and accentuate intra-community inequities[132–134].

While such efforts are important, both for the protection of lions and for addressing the wellbeing costs faced by people living alongside wildlife, it is equally important that the colonial histories of Euro-centric conservation models across lion range are considered[135–138]. Most lions exist in protected areas which were gazetted during colonial regimes for elite sports-hunting across sub-Saharan Africa[139], including the Serengeti National Park. The process of creating these protected areas instigated mass and forced displacement of local communities - often communities that were already marginalised[140]. Many displaced people settled around the outskirts of new “National Parks” that they previously lived within, often in much lower quality areas for arable and livestock farming, and in closer contact with wild predators[141]. As such “fortress conservation” models (intended to protect pristine natural areas) and those who implemented them were responsible for driving increased conflict between people and wildlife[140,142].

In isolation, and without critically examining conservation’s colonial history, present-day dynamics can position rural communities as the enemy of conservation[143]. This is particularly important to consider within the sphere of lion conservation, given the immense cultural significance and charisma of the species globally[144]. As such, public engagement in the discourse around lion conservation is extremely high even outside of the species’ natural range, especially in the Global North[145,146]. Such publics’ sentiments regarding lion conservation management are important because they can impact the flow of money and support to lion range countries - which are needed given the high estimated cost of protecting African lions[147]. However, conservation decision-making is not solely dependent on scientific evidence, and public bodies may form judgements about conservation priorities and policy based on multiple factors[148–150]. Additional complexities exist within the realm of lion conservation as management strategies are often ethically controversial[151] and can be monopolised by political movements to garner support, with trophy hunting being the classic example of this[145,152–154].

### 1.4.5. The role of social media and identity-bias

Increasingly, people use social media to engage in topics of interest to them, including lion conservation[145,152,155]. While this allows for the rapid spread of information, which could benefit species conservation efforts, misinformation is prolific as the credibility of science-related posts can be hard to deduce[156,157]. In addition, divisive debates are common on social media, regularly echoing harmful conservation narratives about poaching and population growth that villainise local communities[158]. Descent into violent, racist, rhetoric directed towards those perceived to be harming wildlife has been evidenced[159]. Such discourse dynamics are often neo-colonial, especially when directed from publics in the Global North towards conservation scenarios and actors in the Global South.

Understanding factors that contribute to such public perceptions of conservation scenarios and actors on social media platforms remains understudied. Message framing is a growing area of research in the conservation sphere[160]. It is broadly understood that the way in which an issue is communicated can impact people's judgement of and response to the problem, tangibly impacting behaviour and engagement[161]. Positively framed messages have proven to garner increased support[162–164]. In addition, individuals' characteristics have been shown to impact perceptions of the acceptability of trophy hunting, as does the framing of the hunt regarding the focal species, economic outcome, and use of the meat[165]. Limited evidence also suggest that the individual messenger can impact engagement and outcomes, particularly if the messenger is a known public figure or researcher[166,167]. However, research so far has not fully investigated how conservation messengers are perceived on social media platforms, especially in combination with other factors known to bias social media engagement, such as identity-bias.

People inherently judge individuals based on their identity, due to societal prejudices against the groups into which they categorise them (referred to throughout as identity-bias)[168]. Gender and race biases are prevalent and well researched in news studies. Typically, women and journalists of colour are underrepresented as experts or sources of information, and particularly strong biases exist against women of colour[169]. The gender and race of broadcasters has been found to impact their perceived objectivity on X (formerly Twitter)[170]. The propensity to follow social media accounts has further been shown to correlate with the profile holder's attractiveness, perceptions of which are influenced by the intersection of their race and gender[170]. Within a conservation context the propensity for such identity-biases to influence public opinion in debates on social media remains untested. However, it is plausible the societal biases could interact with conservation's colonial history to reproduce historic inequities[137] and influence the voices heard, alongside the conservation strategies that receive public support. Such dynamics are reflected in public exposure to conservation experts in popular media who are predominantly white, western individuals[146,171,172]. As such, cycles of inequity are compounded by conservation's persistent lack of "diversity"[173,174].

The need to increase the diversity of perspectives in conservation, and related fields such as ecology, is increasingly being recognised[175–178]. Historically, value has been placed on scientific qualifications and academic achievements over and above Indigenous knowledge and lived or practical experience[163,179–181], promoting parachute science[182]. In addition, the academic conservation space is exclusionary to individuals from marginalised backgrounds, due to barriers that limit access and opportunities based on socio-economic factors. Conservation as an industry is highly competitive, meaning entry to degree programs and job recruitment can be dependent on unpaid labour[183,184], existing social networks[185], and broader experience or hobbies that evidence engagement with nature. Self-promotion and networking are key to increasing collaborative opportunities, which may aid future access to funding and so continual professional development. Conferences and scientific publishing are important for this but can carry huge financial costs[186–188]. Conferences may be additionally prohibitive to conservationists from the Global South due to inequities in visa processes[189].

While individually colonial conservation narratives, public perceptions of conservationists, and barriers to accessing conservation spaces are recognised as problematic, the interconnected nature of these issues remains unaddressed. Further, conservation scientists and practitioners lack actionable suggestions towards overcoming such cycles of injustice. The future of the African lion will depend on the conservation community's ability to centre justice for local communities, incorporate local priorities for species and land-management, remould our communication strategies, and remove barriers to access for marginalised people.

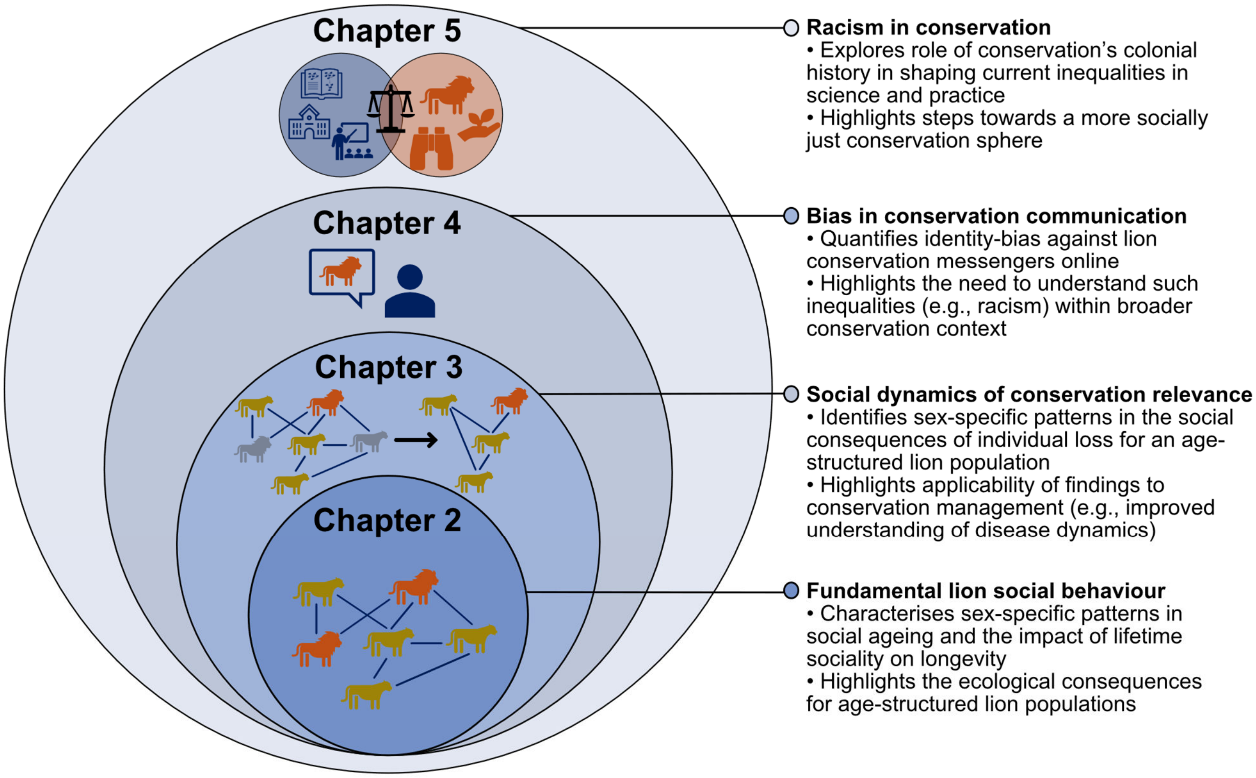
### 1.4.6. Thesis in context

This thesis brings together approaches and methodologies traditionally associated with either behavioural ecology or conservation, to provide a more holistic view of the complex system of lion behaviour and conservation. The research presented in **Chapters 2 – 5** addresses key knowledge gaps related to lion sociality, identity-bias in science communication, and systemic inequalities in conservation science and practice.

Behavioural ecology and conservation are inter-related fields, as understanding the way individuals interact with each other and their environment can help to inform effective conservation strategies[190,191]. This is evident across a breadth of systems and areas, including behavioural responses to environmental change[192,193], spatial behaviour[194,195], and social behaviour[124,196,197]. Social ageing has significant potential in its application to conservation, as it could provide explanations for non-linear population growth and decline (e.g., due to survival or reproduction rates) in age-structured populations[198]. In addition, under increasing environmental and anthropogenic pressure in natural systems, it is imperative to understand the individual and population-level consequences of individual loss across age groups (and not only the loss of aged individuals). Such dynamics are of particular relevance in highly social species of conservation concern, such as the African lion. However, the applicability of behavioural research to conservation has been criticised for being limited by small sample sizes, the use of study species with limited conservation relevance, and a focus on individuals rather than population-wide dynamics[199,200]. In utilising the long-term Serengti lion data set for the behavioural research in Chapters 2 and 3 of this thesis, these barriers to conservation management applications of the results are overcome.

Given the potential applicability of the behavioural ecology research presented in this thesis to lion conservation management, it is important that the human-dynamics of such lion conservation landscapes are considered within the body of work. This should include acknowledgment of factors influencing public engagement with lion conservation, as well as the societal context (past and present) within which all lion behavioural ecology and conservation research is situated. There has been growing recognition of the need to prioritise social justice, equality, and inclusion within conservation and parallel disciplines such as ecology, particularly in academic spaces[175–178]. As such, this thesis first advances knowledge in the emerging discipline of social ageing, before examining vital components of the wider system (including racism, social inequity, and histories of colonialism) that the research was conducted, and will be interpreted, within.

Figure 3 illustrates the conceptual framework that underpins this connection between thesis chapters. It highlights the progression of research from fundamental lion behavioural ecology relevant to species management, to factors influencing public perceptions of lion conservation strategies, to the wider societal context that underpins all lion behavioural ecology and conservation research. It is worth noting that although Chapter 5 primarily focuses on racism in the conservation discipline, its relevance extends to parallel fields (such as behavioural ecology), as well as the broader academic community. This is evident in the vast diversity of citations it has received (as examples, see[201–205]). Accordingly, this thesis is presented as a cohesive body of work in the hope of encouraging continued interdisciplinary research within the sphere of lion behaviour and conservation.



**Racism in conservation**
- Explores role of conservation's colonial history in shaping current inequalities in science and practice
- Highlights steps towards a more socially just conservation sphere

**Bias in conservation communication**
- Quantifies identity-bias against lion conservation messengers online
- Highlights the need to understand such inequalities (e.g., racism) within broader conservation context

**Social dynamics of conservation relevance**
- Identifies sex-specific patterns in the social consequences of individual loss for an age-structured lion population
- Highlights applicability of findings to conservation management (e.g., improved understanding of disease dynamics)

**Fundamental lion social behaviour**
- Characterises sex-specific patterns in social ageing and the impact of lifetime sociality on longevity
- Highlights the ecological consequences for age-structured lion populations

**Figure 3. Conceptual thesis framework and overview.** Circles represent Chapters 2-5 of the thesis, with graphics illustrating the main research themes of each. The circles are nested to highlight the way each thesis chapter grows from the research of the prior chapter, while maintaining connection to the holistic body of work. The larger circle of Chapter 5, encompassing all other chapters, represents the vital contextualisation it provides for the thesis as a whole. Each circle is complemented by text which outlines the main finding of the chapter, plus the key thematic link to the subsequent chapter and broader thesis.

## 1.5. References

1. Milner, H.R. (2007). Race, Culture, and Researcher Positionality: Working Through Dangers Seen, Unseen, and Unforeseen. Educational Researcher *36*, 388–400. https://doi.org/10.3102/0013189X07309471.

2. Beaty, F., Domínguez-Sánchez, P.S., Nalven, K.B., Palacios-Abrantes, J., Oken, K.L., Ban, N.C., Nickols, K.J., Juanes, F., Okey, T.A., Spalding, A.K., et al. (2024). Centering relationships to place for more meaningful research and engagement. Proc. Natl. Acad. Sci. U.S.A. *121*, e2306991121. https://doi.org/10.1073/pnas.2306991121.

3. Oswald, F. (2024). Positionality statements should not force us to ‘out’ ourselves. Nat Hum Behav. https://doi.org/10.1038/s41562-023-01812-5.

4. Gani, J.K., and Khan, R.M. (2024). Positionality Statements as a Function of Coloniality: Interrogating Reflexive Methodologies. International Studies Quarterly *68*, sqae038. https://doi.org/10.1093/isq/sqae038.

5. Crook, J.H., Ellis, J.E., and Goss-Custard, J.D. (1976). Mammalian social systems: Structure and function. Animal Behaviour *24*, 261–274. https://doi.org/10.1016/S0003-3472(76)80035-8.

6. Kappeler, P.M., Barrett, L., Blumstein, D.T., and Clutton-Brock, T.H. (2013). Constraints and flexibility in mammalian social behaviour: introduction and synthesis. Phil. Trans. R. Soc. B *368*, 20120337. https://doi.org/10.1098/rstb.2012.0337.

7. Kappeler, P.M., and van Schaik, C.P. (2002). Evolution of Primate Social Systems. International Journal of Primatology.

8. Clutton-Brock, T.H. Review Lecture: Mammalian mating systems. Proceedings of the Royal Society B: Biological Sciences *236*, 339–372.

9. Hinde, R.A. (1976). Interactions, Relationships and Social Structure. Man *11*, 1. https://doi.org/10.2307/2800384.

10. Shizuka, D., and Johnson, A.E. (2020). How demographic processes shape animal social networks. Behavioral Ecology *31*, 1–11. https://doi.org/10.1093/beheco/arz083.

11. Wilson, E.O. (1975). Sociobiology: the new synthesis (Harvard University Press).

12. Lusseau, D. (2003). The emergent properties of a dolphin social network. Proceedings of the Royal Society B: Biological Sciences *270*, 186–188. https://doi.org/10.1098/rsbl.2003.0057.

13. Croft, D.P., James, R., Ward, A.J.W., Botham, M.S., Mawdsley, D., and Krause, J. (2005). Assortative interactions and social networks in fish. Oecologia *143*, 211–219. https://doi.org/10.1007/s00442-004-1796-8.

14. Lusseau, D., and Newman, M.E.J. (2004). Identifying the role that animals play in their social networks. Proc. R. Soc. Lond. B *271*. https://doi.org/10.1098/rsbl.2004.0225.

15. Croft, D.P., Krause, J., and James, R. (2004). Social networks in the guppy ( *Poecilia reticulata* ). Proc. R. Soc. Lond. B *271*. https://doi.org/10.1098/rsbl.2004.0206.

16. Krause, J., James, R., Franks, D.W., and Croft, D.P. (2015). Animal Social Networks (Oxford University Press).

17. Brandell, E.E., Fountain-Jones, N.M., Gilbertson, M.L.J., Cross, P.C., Hudson, P.J., Smith, D.W., Stahler, D.R., Packer, C., and Craft, M.E. (2020). Group density, disease, and season shape territory size and overlap of social carnivores. Journal of Animal Ecology, 1–15. https://doi.org/10.1111/1365-2656.13294.

18. Farine, D.R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology *84*, 1144–1163. https://doi.org/10.1111/1365-2656.12418.

19. Croft, D.P., Madden, J.R., Franks, D.W., and James, R. (2011). Hypothesis testing in animal social networks. Trends in Ecology & Evolution *26*, 502–507. https://doi.org/10.1016/j.tree.2011.05.012.

20. Rushmore, J., Caillaud, D., Matamba, L., Stumpf, R.M., Borgatti, S.P., and Altizer, S. (2013). Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. Journal of Animal Ecology *82*, 976–986. https://doi.org/10.1111/1365-2656.12088.

21. Albery, G.F., Kirkpatrick, L., Firth, J.A., and Bansal, S. (2021). Unifying spatial and social network analysis in disease ecology. Journal of Animal Ecology *90*, 45–61. https://doi.org/10.1111/1365-2656.13356.

22. Silk, M.J., Croft, D.P., Delahay, R.J., Hodgson, D.J., Boots, M., Weber, N., and McDONALD, R.A. (2017). Using social network measures in wildlife disease ecology, epidemiology, and management. BioScience *67*, 245–257. https://doi.org/10.1093/biosci/biw175.

23. Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. Proceedings of

the Royal Society B: Biological Sciences *279*, 4199–4205. https://doi.org/10.1098/rspb.2012.1591.

24. Boogert, N.J., Nightingale, G.F., Hoppitt, W., and Laland, K.N. (2014). Perching but not foraging networks predict the spread of novel foraging skills in starlings. Behavioural Processes *109*, 135–144. https://doi.org/10.1016/j.beproc.2014.08.016.

25. Chiyo, P.I., Moss, C.J., and Alberts, S.C. (2012). The influence of life history milestones and association networks on crop-raiding behavior in male african elephants. PLoS ONE *7*. https://doi.org/10.1371/journal.pone.0031382.

26. Crofoot, M.C., Rubenstein, D.I., Maiya, A.S., and Berger-Wolf, T.Y. (2011). Aggression, grooming and group-level cooperation in white-faced capuchins (Cebus capucinus): Insights from social networks. American Journal of Primatology *73*, 821–833. https://doi.org/10.1002/ajp.20959.

27. Blonder, B., Wey, T.W., Dornhaus, A., James, R., and Sih, A. (2012). Temporal dynamics and network analysis. Methods Ecol Evol *3*, 958–972. https://doi.org/10.1111/j.2041-210X.2012.00236.x.

28. Blonder, B., and Dornhaus, A. (2011). Time-ordered networks reveal limitations to information flow in ant colonies. PLoS ONE *6*, 1–8. https://doi.org/10.1371/journal.pone.0020298.

29. Murphy, D., Mumby, H.S., and Henley, M.D. (2019). Age differences in the temporal stability of a male African elephant (Loxodonta africana) social network. Behavioral Ecology, arz152. https://doi.org/10.1093/beheco/arz152.

30. Aplin, L.M., Firth, J.A., Farine, D.R., Voelkl, B., Crates, R.A., Culina, A., Garroway, C.J., Hinde, C.A., Kidd, L.R., Psorakis, I., et al. (2015). Consistent individual differences in the social phenotypes of wild great tits, Parus major. Animal Behaviour *108*, 117–127. https://doi.org/10.1016/j.anbehav.2015.07.016.

31. Shizuka, D., Chaine, A.S., Anderson, J., Johnson, O., Laursen, I.M., and Lyon, B.E. (2014). Across-year social stability shapes network structure in wintering migrant sparrows. Ecology Letters *17*, 998–1007. https://doi.org/10.1111/ele.12304.

32. Jones, T.B., Green, J.A., Patrick, S.C., Evans, J.C., Wells, M.R., Rodríguez-Malagón, M.A., and Arnould, J.P.Y. (2020). Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. Ecology Letters *23*, 1085–1096. https://doi.org/10.1111/ele.13507.

33. Maldonado-Chaparro, A.A., Montiglio, P., Forstmeier, W., Kempenaers, B., and Farine, D.R. (2018). Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biological Reviews *93*, 1558–1577. https://doi.org/10.1111/brv.12408.

34. Nicolaus, M., Michler, S.P.M., Jalvingh, K.M., Ubels, R., Van Der Velde, M., Komdeur, J., Both, C., and Tinbergen, J.M. (2012). Social environment affects juvenile dispersal in great tits ( *Parus major* ). Journal of Animal Ecology *81*, 827–837. https://doi.org/10.1111/j.1365-2656.2012.01959.x.

35. Wey, T.W., Spiegel, O., Montiglio, P.-O., and Mabry, K.E. (2015). Natal dispersal in a social landscape: Considering individual behavioral phenotypes and social environment in dispersal ecology. Current Zoology *61*, 543–556. https://doi.org/10.1093/czoolo/61.3.543.

36. Vercken, E., Sinervo, B., and Clobert, J. (2012). The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment. Behavioral Ecology *23*, 1059–1067. https://doi.org/10.1093/beheco/ars075.

37. Payne, E., Spiegel, O., Sinn, D.L., Leu, S.T., Gardner, M.G., Godfrey, S.S., Wohlfeil, C., and Sih, A. (2022). Intrinsic traits, social context, and local environment shape home range size and fidelity of sleepy lizards. Ecological Monographs *92*, e1519. https://doi.org/10.1002/ecm.1519.

38. Macdonald, D.W., and Johnson, D.D.P. (2015). Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. Journal of Zoology *295*, 75–107. https://doi.org/10.1111/jzo.12202.

39. Webber, Q.M.R., Albery, G.F., Farine, D.R., Pinter-Wollman, N., Sharma, N., Spiegel, O., Vander Wal, E., and Manlove, K. (2023). Behavioural ecology at the spatial–social interface. Biological Reviews *98*, 868–886. https://doi.org/10.1111/brv.12934.

40. Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2022). Ageing red deer alter their spatial behaviour and become less social. Nat Ecol Evol *6*, 1231–1238. https://doi.org/10.1038/s41559-022-01817-9.

41. Albery, G.F., Morris, A., Morris, S., Pemberton, J.M., Clutton-Brock, T.H., Nussey, D.H., and Firth, J.A. (2021). Multiple spatial behaviours govern social network positions in a wild ungulate. Ecology Letters *24*, 676–686. https://doi.org/10.1111/ele.13684.

42. Gokcekus, S., Firth, J.A., Cole, E.F., Sheldon, B.C., and Albery, G.F. (2024). Different types of social links contrastingly shape reproductive wellbeing in a multi-level society of wild songbirds. Preprint, https://doi.org/10.1101/2024.02.02.578606 https://doi.org/10.1101/2024.02.02.578606.

43. Albery, G.F., Newman, C., Ross, J.B., MacDonald, D.W., Bansal, S., and Bueshing, C. (2020). Negative density-dependent parasitism in a group-living carnivore. Proceedings of the Royal Society B: Biological Sciences *287*.

44. Banks, S.C., Piggott, M.P., Stow, A.J., and Taylor, A.C. (2007). Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactionsThis review is one of a series dealing with some aspects of the impact of habitat fragmentation on animals and plants. This series is one of several virtual symposia focussing on ecological topics that will be published in the Journal from time to time. Can. J. Zool. *85*, 1065–1079. https://doi.org/10.1139/Z07-094.

45. Komdeur, J., and Ma, L. (2021). Keeping up with environmental change: The importance of sociality. Ethology *127*, 790–807. https://doi.org/10.1111/eth.13200.

46. Koenig, A., Scarry, C.J., Wheeler, B.C., and Borries, C. (2013). Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. Phil. Trans. R. Soc. B *368*, 20120348. https://doi.org/10.1098/rstb.2012.0348.

47. Reeve, H.K., and Shellman-Reeve, J.S. (1997). The general protected invasion theory: Sex biases in parental and alloparental care. Evolutionary Ecology *11*, 357–370. https://doi.org/10.1023/A:1018472521277.

48. Clutton-Brock, T.H., and Huchard, E. (2013). Social competition and selection in males and females. Phil. Trans. R. Soc. B *368*, 20130074. https://doi.org/10.1098/rstb.2013.0074.

49. Blaszczyk, M.B. (2018). Consistency in social network position over changing environments in a seasonally breeding primate. Behav Ecol Sociobiol *72*, 11. https://doi.org/10.1007/s00265-017-2425-y.

50. Ramos-Fernández, G., Boyer, D., Aureli, F., and Vick, L.G. (2009). Association networks in spider monkeys (Ateles geoffroyi). Behav Ecol Sociobiol *63*, 999–1013. https://doi.org/10.1007/s00265-009-0719-4.

51. Krzyszczyk, E., Patterson, E.M., Stanton, M.A., and Mann, J. (2017). The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins. Animal Behaviour *129*, 43–59. https://doi.org/10.1016/j.anbehav.2017.04.011.

52. Spiegel, O., Sih, A., Leu, S.T., and Bull, C.M. (2018). Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure. Animal Behaviour *136*, 207–215. https://doi.org/10.1016/j.anbehav.2017.11.001.

53. Kalbitzer, U., and Chapman, C.A. (2021). Patterns of female social relationships in a primate with female-biased dispersal. Animal Behaviour *177*, 117–133. https://doi.org/10.1016/j.anbehav.2021.04.024.

54. De Moor, D., Roos, C., Ostner, J., and Schülke, O. (2020). Bonds of bros and brothers: Kinship and social bonding in postdispersal male macaques. Molecular Ecology *29*, 3346–3360. https://doi.org/10.1111/mec.15560.

55. Elliot, N.B., Valeix, M., Macdonald, D.W., and Loveridge, A.J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. Oikos *123*, 1049–1056. https://doi.org/10.1111/oik.01266.

56. Patriquin, K.J., Leonard, M.L., Broders, H.G., and Garroway, C.J. (2010). Do social networks of female northern long-eared bats vary with reproductive period and age? Behav Ecol Sociobiol *64*, 899–913. https://doi.org/10.1007/s00265-010-0905-4.

57. Wey, T.W., and Blumstein, D.T. (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. Animal Behaviour *79*, 1343–1352. https://doi.org/10.1016/j.anbehav.2010.03.008.

58. Carter, K.D., Brand, R., Carter, J.K., Shorrocks, B., and Goldizen, A.W. (2013). Social networks, long-term associations and age-related sociability of wild giraffes. Animal Behaviour *86*, 901–910. https://doi.org/10.1016/j.anbehav.2013.08.002.

59. Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Emery Thompson, M., Muller, M.N., Wrangham, R.W., and Machanda, Z.P. (2020). Social selectivity in aging wild chimpanzees. Science *370*, 473–476. https://doi.org/10.1126/science.aaz9129.

60. Nussey, D.H. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing Research Reviews.

61. Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M., and Gaillard, J.-M. (2011). Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. Ecology *92*, 1936–1947. https://doi.org/10.1890/11-0308.1.

62. Lemaître, J., and Gaillard, J. (2017). Reproductive senescence: new perspectives in the wild. Biological Reviews *92*, 2182–2199. https://doi.org/10.1111/brv.12328.

63. Weladji, R.B., Holand, Ø., Gaillard, J.-M., Yoccoz, N.G., Mysterud, A., Nieminen, M., and Stenseth, N.C. (2010). Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? Oecologia *162*, 261–271. https://doi.org/10.1007/s00442-009-1443-5.

64. Packer, C., Tatar, M., and Collins, A. (1998). Reproductive cessation in female mammals. Nature *392*, 807–811. https://doi.org/10.1038/33910.

65. MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R., and Packer, C. (2009). Predatory senescence in ageing wolves. Ecology Letters *12*, 1347–1356. https://doi.org/10.1111/j.1461-0248.2009.01385.x.

66. Catry, P., Phillips, R.A., Phalan, B., and Croxall, J.P. (2006). Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. Proc. R. Soc. B. *273*, 1625–1630. https://doi.org/10.1098/rspb.2006.3482.

67. Albery, G.F., Sweeny, A.R., and Webber, Q. (2023). How behavioural ageing affects infectious disease. Neuroscience & Biobehavioral Reviews *155*, 105426. https://doi.org/10.1016/j.neubiorev.2023.105426.

68. Palacios, M.G., Winkler, D.W., Klasing, K.C., Hasselquist, D., and Vleck, C.M. (2011). Consequences of immune system aging in nature: a study of immunosenescence costs in free-living Tree Swallows. Ecology *92*, 952–966. https://doi.org/10.1890/10-0662.1.

69. Nussey, D.H., Watt, K., Pilkington, J.G., Zamoyska, R., and McNeilly, T.N. (2012). Age-related variation in immunity in a wild mammal population. Aging Cell *11*, 178–180. https://doi.org/10.1111/j.1474-9726.2011.00771.x.

70. Siracusa, E.R., Pavez-Fox, M.A., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Snyder-Mackler, N., Higham, J.P., Brent, L.J.N., and Silk, M.J. (2024). Social ageing can protect against infectious disease in a group-living primate. Preprint, https://doi.org/10.1101/2024.03.09.584237 https://doi.org/10.1101/2024.03.09.584237.

71. Woodman, J., Gokcekus, S., Beck, K., Green, J., Nussey, D., and Firth, J. (2024). The ecology of ageing in wild societies: linking age structure and social behaviour in natural populations (Life Sciences) https://doi.org/10.32942/X21893.

72. Siracusa, E.R., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. Biol. Lett. *18*, 20210643. https://doi.org/10.1098/rsbl.2021.0643.

73. Siracusa, E.R., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Within-individual changes reveal increasing social selectivity with age in rhesus macaques. Proc. Natl. Acad. Sci. U.S.A. *119*, e2209180119. https://doi.org/10.1073/pnas.2209180119.

74. Larson, S.M., Ruiz-Lambides, A., Platt, M.L., and Brent, L.J.N. (2018). Social network dynamics precede a mass eviction in group-living rhesus macaques. Animal Behaviour *136*, 185–193. https://doi.org/10.1016/j.anbehav.2017.08.019.

75. Thompson, F.J., Marshall, H.H., Vitikainen, E.I.K., Young, A.J., and Cant, M.A. (2017). Individual and demographic consequences of mass eviction in cooperative banded mongooses. Animal Behaviour *134*, 103–112. https://doi.org/10.1016/j.anbehav.2017.10.009.

76. Schneidman, S.A., Philson, C.S., and Blumstein, D.T. (2024). Extending the social cohesion hypothesis: is group social structure associated with dispersal in yellow-bellied marmots ( *Marmota flaviventer* )? Current Zoology, zoae002. https://doi.org/10.1093/cz/zoae002.

77. Evans, J.C., Liechti, J.I., Boatman, B., and König, B. (2020). A natural catastrophic turnover event: Individual sociality matters despite community resilience in wild

house mice. Proceedings of the Royal Society B: Biological Sciences *287*, 1–9. https://doi.org/10.1098/rspb.2019.2880.

78. Testard, C., Larson, S.M., Watowich, M., Kaplinsky, C.H., Bernau, A., Faulder, M., Ruiz-Lambides, A., Higham, J.P., Montague, M., Snyder-Mackler, N., et al. (2020). Rhesus Macaques Build New Social Connections after a Natural Disaster. SSRN Electronic Journal, 1–11. https://doi.org/10.2139/ssrn.3741230.

79. Goldenberg, S.Z., Douglas-Hamilton, I., and Wittemyer, G. (2016). Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks. Current Biology *26*, 75–79. https://doi.org/10.1016/j.cub.2015.11.005.

80. Firth, J.A., Voelkl, B., Crates, R.A., Aplin, L.M., Biro, D., Croft, D.P., and Sheldon, B.C. (2017). Wild birds respond to flockmate loss by increasing their social network associations to others. Proceedings of the Royal Society B: Biological Sciences *284*. https://doi.org/10.1098/rspb.2017.0299.

81. Downing, B.C., Silk, M.J., Delahay, R.J., Bearhop, S., and Royle, N.J. (2023). Culling-induced perturbation of social networks of wild geese reinforces rather than disrupts associations among survivors. Journal of Applied Ecology *60*, 2613–2624. https://doi.org/10.1111/1365-2664.14522.

82. Williams, R., and Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. Biology Letters *2*, 497–500. https://doi.org/10.1098/rsbl.2006.0510.

83. Busson, M., Authier, M., Barbraud, C., Tixier, P., Reisinger, R.R., Janc, A., and Guinet, C. (2019). Role of sociality in the response of killer whales to an additive mortality event. Proceedings of the National Academy of Sciences of the United States of America *116*, 11812–11817. https://doi.org/10.1073/pnas.1817174116.

84. McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J., and Moss, C. (2011). Leadership in elephants: the adaptive value of age. Proc. R. Soc. B. *278*, 3270–3276. https://doi.org/10.1098/rspb.2011.0168.

85. Brent, L.J.N., Franks, D.W., Foster, E.A., Balcomb, K.C., Cant, M.A., and Croft, D.P. (2015). Ecological Knowledge, Leadership, and the Evolution of Menopause in Killer Whales. Current Biology *25*, 746–750. https://doi.org/10.1016/j.cub.2015.01.037.

86. Firth, J.A. (2020). Considering Complexity: Animal Social Networks and Behavioural Contagions. Trends in Ecology and Evolution *35*, 100–104. https://doi.org/10.1016/j.tree.2019.10.009.

87. Lucas, E.R., and Keller, L. (2020). The co-evolution of longevity and social life. Functional Ecology *34*, 76–87. https://doi.org/10.1111/1365-2435.13445.

88. Holt-Lunstad, J., Smith, T.B., and Layton, J.B. (2010). Social Relationships and Mortality Risk: A Meta-analytic Review. PLoS Medicine *7*. https://doi.org/doi:10.1371/ journal.pmed.1000316.

89. Ball, K., Jeffery, R.W., Abbott, G., McNaughton, S.A., and Crawford, D. (2010). Is healthy behavior contagious: associations of social norms with physical activity and healthy eating. Int J Behav Nutr Phys Act *7*, 86. https://doi.org/10.1186/1479-5868-7-86.

90. Berkman, L.F. (1995). The Role of Social Relations in Health Promotion: Psychosomatic Medicine *57*, 245–254. https://doi.org/10.1097/00006842-199505000-00006.

91. Kikusui, T., Winslow, J.T., and Mori, Y. (2006). Social buffering: relief from stress and anxiety. Phil. Trans. R. Soc. B *361*, 2215–2228. https://doi.org/10.1098/rstb.2006.1941.

92. Pavez-Fox, M.A., Kimock, C.M., Rivera-Barreto, N., Negron-Del Valle, J.E., Phillips, D., Ruiz-Lambides, A., Snyder-Mackler, N., Higham, J.P., Siracusa, E.R., and Brent, L.J.N. (2022). Reduced injury risk links sociality to survival in a group-living primate. iScience *25*, 105454. https://doi.org/10.1016/j.isci.2022.105454.

93. Pavez-Fox, M.A., Negron-Del Valle, J.E., Thompson, I.J., Walker, C.S., Bauman, S.E., Gonzalez, O., Compo, N., Ruiz-Lambides, A., Martinez, M.I., Platt, M.L., et al. (2021). Sociality predicts individual variation in the immunity of free-ranging rhesus macaques. Physiology & Behavior *241*, 113560. https://doi.org/10.1016/j.physbeh.2021.113560.

94. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. Current Biology *20*, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067.

95. Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M.L., and Brent, L.J.N. (2019). Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. Proc. R. Soc. B. *286*, 20191991. https://doi.org/10.1098/rspb.2019.1991.

96. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc. R. Soc. B. *276*, 3099–3104. https://doi.org/10.1098/rspb.2009.0681.

97. Archie, E.A., Tung, J., Clark, M., Altmann, J., and Alberts, S.C. (2014). Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. Proceedings of the Royal Society B: Biological Sciences *281*. https://doi.org/10.1098/rspb.2014.1261.

98. Frère, C.H., Krützen, M., Mann, J., Connor, R.C., Bejder, L., and Sherwin, W.B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. Proc. Natl. Acad. Sci. U.S.A. *107*, 19949–19954. https://doi.org/10.1073/pnas.1007997107.

99. Cameron, E.Z., Setsaas, T.H., and Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. Proceedings of the National Academy of Sciences of the United States of America *106*, 13850–13853. https://doi.org/10.1073/pnas.0900639106.

100. Packer, C. (2023). The Lion: Behvaiour, ecology and conservation of an iconic species (Princeton University Press).

101. Mahony, J., Dyer, E., and Washington, R. (2021). The precipitation patterns and atmospheric dynamics of the Serengeti National Park. Intl Journal of Climatology *41*. https://doi.org/10.1002/joc.6831.

102. Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., and Sinclair, A.R.E. (2005). Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. Most, 390–393.

103. Durant, S.M., Caro, T.M., Collins, D.A., Alawi, R.M., and Fitzgibbon, C.D. (1988). Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. African Journal of Ecology *26*, 257–268. https://doi.org/10.1111/j.1365-2028.1988.tb00978.x.

104. Larsen, F., Hopcraft, J.G.C., Hanley, N., Hongoa, J.R., Hynes, S., Loibooki, M., Mafuru, G., Needham, K., Shirima, F., and Morrison, T.A. (2020). Wildebeest migration drives tourism demand in the Serengeti. Biological Conservation *248*, 108688. https://doi.org/10.1016/j.biocon.2020.108688.

105. Packer, C., Scheel, D., and Pusey, A.E. (1990). Why Lions Form Groups : Food is Not Enough Author. The American naturalist *136*, 1–19.

106. VanderWaal, K.L., Mosser, A., and Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Animal Behaviour *77*, 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028.

107. Pusey, A.E., and Packer, C. (1987). The Evolution of Sex-Biased Dispersal in Lions. Behav *101*, 275–310. https://doi.org/10.1163/156853987X00026.

108. Bygott, J.D., Bertram, B.C.R., and Hanby, J.P. (1979). Male lions in large coalitions gain reproductive advantages. Nature *282*, 839–841. https://doi.org/10.1038/282839a0.

109. Borrego, N., Ozgul, A., Slotow, R., and Packer, C. (2018). Lion population dynamics: do nomadic males matter? Behavioral Ecology *29*, 660–666. https://doi.org/10.1093/beheco/ary018.

110. Packer, C., Pusey, A.E., and Eberly, L.E. (2001). Egalitarianism in female African lions. Science *293*, 690–693. https://doi.org/10.1126/science.1062320.

111. Mosser, A., Fryxell, J.M., Eberly, L., and Packer, C. (2009). Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. Ecology Letters *12*, 1050–1060. https://doi.org/10.1111/j.1461-0248.2009.01359.x.

112. Pusey, A.E., and Packer, C. (1994). Non-offspring nursing in social carnivores: Minimizing the costs. Behavioral Ecology *5*, 362–374. https://doi.org/10.1093/beheco/5.4.362.

113. Mosser, A., and Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, Panthera leo. Animal Behaviour *78*, 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024.

114. Heinsohn, R., and Packer, C. (1995). Complex Cooperative Strategies in Group-Territorial African Lions. Science *269*, 1260–1262. https://doi.org/10.1126/science.7652573.

115. Scheel, D., and Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. Animal Behaviour *41*, 697–709. https://doi.org/10.1016/S0003-3472(05)80907-8.

116. Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O’Brien, S.J., Pospischil, A., Hofman-Lehmann, R., Lutz, H., et al. (1996). A canine distemper virus epidemic in Serengeti lions (Panthera leo). Nature *379*, 441–445. https://doi.org/10.1038/379441a0.

117. Carpenter, M.A., J.g. Appel, M., Roelke-Parker, M.E., Munson, L., Hofer, H., East, M., and O’Brien, S.J. (1998). Genetic characterization of canine distemper virus in Serengeti carnivores. Veterinary Immunology and Immunopathology *65*, 259–266. https://doi.org/10.1016/S0165-2427(98)00159-7.

118. Guiserix, M., Bahi-Jaber, N., Fouchet, D., Sauvage, F., and Pontier, D. (2007). The canine distemper epidemic in Serengeti: Are lions victims of a new highly virulent canine distemper virus strain, or is pathogen circulation stochasticity to blame? Journal of the Royal Society Interface *4*, 1127–1134. https://doi.org/10.1098/rsif.2007.0235.

119. Munson, L., Terio, K.A., Kock, R., Mlengeya, T., Roelke, M.E., Dubovi, E., Summers, B., Sinclair, A.R.E., and Packer, C. (2008). Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. PLoS ONE *3*, 5–10. https://doi.org/10.1371/journal.pone.0002545.

120. Weckworth, J.K., Davis, B.W., Dubovi, E., Fountain-Jones, N., Packer, C., Cleaveland, S., Craft, M.E., Eblate, E., Schwartz, M., Mills, L.S., et al. (2020). Cross-species transmission and evolutionary dynamics of canine distemper virus

during a spillover in African lions of Serengeti National Park. Molecular Ecology, 1–14. https://doi.org/10.1111/mec.15449.

121. Cleaveland, S., Appel, M.G.J., Chalmers, W.S.K., Chillingworth, C., Kaare, M., and Dye, C. (2000). Serological and demographic evidence for domestic dogs as a source of canine distemper virus infection for Serengeti wildlife. Veterinary Microbiology *72*, 217–227. https://doi.org/10.1016/S0378-1135(99)00207-2.

122. Viana, M., Cleaveland, S., Matthiopoulos, J., Halliday, J., Packer, C., Craft, M.E., Hampson, K., Czupryn, A., Dobson, A.P., Dubovi, E.J., et al. (2015). Dynamics of a morbillivirus at the domestic -wildlife interface: Canine distemper virus in domestic dogs and lions. Proceedings of the National Academy of Sciences of the United States of America *112*, 1464–1469. https://doi.org/10.1073/pnas.1411623112.

123. Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S.K., Sillero-Zubiri, C., Hunter, L., Lindsey, P., and Macdonald, D.W. (2022). Threat analysis for more effective lion conservation. Oryx *56*, 108–115. https://doi.org/10.1017/S0030605320000253.

124. Snijders, L., Blumstein, D.T., Stanley, C.R., and Franks, D.W. (2017). Animal Social Network Theory Can Help Wildlife Conservation. Trends in Ecology and Evolution *32*, 567–577. https://doi.org/10.1016/j.tree.2017.05.005.

125. Nicholson, S.K., Bauer, H., Strampelli, P., Sogbohossou, E., Ikanda, D., Tumenta, P.F., Venktramen, M., Chapron, G., and Loveridge, A. (2023). Panthera leo. The IUCN Red List of Threatened Species *e.T15951A231696234*.

126. Gayo, L., Nahonyo, C.L., and Masao, C.A. (2021). Socioeconomic Factors Influencing Local Community Perceptions Towards Lion Conservation: A Case of the Selous Game Reserve, Tanzania. Journal of Asian and African Studies *56*, 480–494. https://doi.org/10.1177/0021909620929382.

127. Gebresenbet, F., Bauer, H., Vadjunec, J.M., and Papeş, M. (2018). Beyond the numbers: Human attitudes and conflict with lions (Panthera leo) in and around Gambella National Park, Ethiopia. PLoS ONE *13*, e0204320. https://doi.org/10.1371/journal.pone.0204320.

128. Hazzah, L., Bath, A., Dolrenry, S., Dickman, A., and Frank, L. (2017). From Attitudes to Actions: Predictors of Lion Killing by Maasai Warriors. PLoS ONE *12*, e0170796. https://doi.org/10.1371/journal.pone.0170796.

129. Hemson, G., Maclennan, S., Mills, G., Johnson, P., and Macdonald, D. (2009). Community, lions, livestock and money: A spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. Biological Conservation *142*, 2718–2725. https://doi.org/10.1016/j.biocon.2009.06.024.

130. Sibanda, L., Johnson, P.J., Van Der Meer, E., Hughes, C., Dlodlo, B., Mathe, L.J., Hunt, J.E., Parry, R.H., Macdonald, D.W., and Loveridge, A.J. (2022). Effectiveness of community-based livestock protection strategies: a case study of human–lion conflict mitigation. Oryx *56*, 537–545. https://doi.org/10.1017/S0030605321000302.

131. LeFlore, E.G., Fuller, T.K., Tomeletso, M., Dimbindo, T.C., and Stein, A.B. (2020). Human dimensions of human–lion conflict: a pre- and post-assessment of a lion conservation programme in the Okavango Delta, Botswana. Envir. Conserv. *47*, 182–189. https://doi.org/10.1017/S0376892920000120.

132. Anyango-Van Zwieten, N., Van Der Duim, R., and Visseren-Hamakers, I.J. (2015). Compensating for livestock killed by lions: payment for environmental services as a policy arrangement. Envir. Conserv. *42*, 363–372. https://doi.org/10.1017/S0376892915000090.

133. Bauer, H., Müller, L., Van Der Goes, D., and Sillero-Zubiri, C. (2017). Financial compensation for damage to livestock by lions *Panthera leo* on community rangelands in Kenya. Oryx *51*, 106–114. https://doi.org/10.1017/S003060531500068X.

134. Maclennan, S.D., Groom, R.J., Macdonald, D.W., and Frank, L.G. (2009). Evaluation of a compensation scheme to bring about pastoralist tolerance of lions. Biological Conservation *142*, 2419–2427. https://doi.org/10.1016/j.biocon.2008.12.003.

135. Domínguez, L., and Luoma, C. (2020). Decolonising conservation policy: How colonial land and conservation ideologies persist and perpetuate indigenous injustices at the expense of the environment. Land *9*, 11–14. https://doi.org/10.3390/land9030065.

136. Garland, E. (2008). The Elephant in the Room: Confronting the Colonial Character of Wildlife Conservation in Africa. Afr. Stud. Rev. *51*, 51–74. https://doi.org/10.1353/arw.0.0095.

137. Kashwan, P., V. Duffy, R., Massé, F., Asiyanbi, A.P., and Marijnen, E. (2021). From Racialized Neocolonial Global Conservation to an Inclusive and Regenerative Conservation. Environment: Science and Policy for Sustainable Development *63*, 4–19. https://doi.org/10.1080/00139157.2021.1924574.

138. Neumann, R.P. (1995). Ways of Seeing Africa: Colonial Recasting of African Society and Landscape in Serengeti National Park. Ecumene *2*, 149–169. https://doi.org/10.1177/147447409500200203.

139. Munro, P. (2021). Colonial Wildlife Conservation and National Parks in Sub-Saharan Africa. In Oxford Research Encyclopedia of African History (Oxford University Press). https://doi.org/10.1093/acrefore/9780190277734.013.195.

140. Brockington, D., and Igoe, J. (2006). Eviction for Conservation: A Global Overview. Conservation and Society *4*, 424–470.

141. Dowie, M. (2009). Conservation refugees: The hundred-year conflict between global conservation and native peoples (MIT Press).

142. Brockington, D. (2004). Community Conservation, Inequality and Injustice: Myths of Power in Protected Area Management. Conservation and Society *2*, 411–432.

143. De Jong, M., and Butt, B. (2023). Conservation violence: Paradoxes of "making live" and "letting die" in anti-poaching practices. Environment and Planning E: Nature and Space *6*, 2400–2423. https://doi.org/10.1177/25148486231151805.

144. Macdonald, E.A., Burnham, D., Hinks, A.E., Dickman, A.J., Malhi, Y., and Macdonald, D.W. (2015). Conservation inequality and the charismatic cat: Felis felicis. Global Ecology and Conservation *3*, 851–866. https://doi.org/10.1016/j.gecco.2015.04.006.

145. Macdonald, D.W., Jacobsen, K.S., Burnham, D., Johnson, P.J., and Loveridge, A.J. (2016). Cecil: A moment or a movement? Analysis of media coverage of the death of a lion, Panthera Leo. Animals *6*. https://doi.org/10.3390/ani6050026.

146. McCubbin, S.G. (2020). The Cecil Moment: Celebrity environmentalism, Nature 2.0, and the cultural politics of lion trophy hunting. Geoforum *108*, 194–203. https://doi.org/10.1016/j.geoforum.2019.10.015.

147. Lindsey, P.A., Miller, J.R.B., Petracca, L.S., Coad, L., Dickman, A.J., Fitzgerald, K.H., Flyman, M.V., Funston, P.J., Henschel, P., Kasiki, S., et al. (2018). More than $1 billion needed annually to secure Africa's protected areas with lions. Proc. Natl. Acad. Sci. U.S.A. *115*. https://doi.org/10.1073/pnas.1805048115.

148. Duthie, E., Veríssimo, D., Keane, A., and Knight, A.T. (2017). The effectiveness of celebrities in conservation marketing. PLoS ONE *12*, e0180027. https://doi.org/10.1371/journal.pone.0180027.

149. Massingham, E.J., Wilson, K.A., Meijaard, E., Ancrenaz, M., Santika, T., Friedman, R., Possingham, H.P., and Dean, A.J. (2023). Public opinion on protecting iconic species depends on individual wellbeing: Perceptions about orangutan conservation in Indonesia and Malaysia. Environmental Science & Policy *150*, 103588. https://doi.org/10.1016/j.envsci.2023.103588.

150. Wright, A.J., Veríssimo, D., Pilfold, K., Parsons, E.C.M., Ventre, K., Cousins, J., Jefferson, R., Koldewey, H., Llewellyn, F., and McKinley, E. (2015). Competitive outreach in the 21st century: Why we need conservation marketing. Ocean & Coastal Management *115*, 41–48. https://doi.org/10.1016/j.ocecoaman.2015.06.029.

151. Vucetich, J.A., Burnham, D., Johnson, P.J., Loveridge, A.J., Nelson, M.P., Bruskotter, J.T., and Macdonald, D.W. (2019). The value of argument analysis for understanding ethical considerations pertaining to trophy hunting and lion conservation. Biological Conservation *235*, 260–272. https://doi.org/10.1016/j.biocon.2019.04.012.

152. Chimuka, G. (2022). The role of the media and the international community in recent conservation issues in Sourthern Africa: The case of Cecil the lion. In Protected Areas and Tourism in Southern Africa (Routledge), pp. 146–160.

153. Hart, A.G., Cooney, R., Dickman, A., Hare, D., Jonga, C., Johnson, P.K., Louis, M.P., Lubilo, R., Roe, D., Semcer, C., et al. (2020). Threats posed to conservation by media misinformation. Conservation Biology *34*, 1333–1334. https://doi.org/10.1111/cobi.13605.

154. Nelson, M.P., Bruskotter, J.T., Vucetich, J.A., and Chapron, G. (2016). Emotions and the Ethics of Consequence in Conservation Decisions: Lessons from Cecil the Lion: Emotions and ethics in conservation decisions. CONSERVATION LETTERS *9*, 302–306. https://doi.org/10.1111/conl.12232.

155. Evans, L.C., Greenwell, M.P., Boult, V.L., and Johnson, T.F. (2023). Characterizing the trophy hunting debate on Twitter. Conservation Biology *37*, e14070. https://doi.org/10.1111/cobi.14070.

156. Yang, K.C., Pierri, F., Hui, P.M., Axelrod, D., Torres-Lugo, C., Bryden, J., and Menczer, F. (2021). The COVID-19 Infodemic: Twitter versus Facebook. Big Data and Society *8*. https://doi.org/10.1177/20539517211013861.

157. Vosoughi, S., Roy, D., and Aral, S. (2018). The spread of true and false news online. Science *359*, 1146–1151. https://doi.org/10.1126/science.aap9559.

158. Mkono, M. (2022). How we can make the trophy hunting debate less fraught. Nat Hum Behav *7*, 6–8. https://doi.org/10.1038/s41562-022-01488-3.

159. Lunstrum, E. (2017). Feed them to the lions: Conservation violence goes online. Geoforum *79*, 134–143. https://doi.org/10.1016/j.geoforum.2016.04.009.

160. Kidd, L.R., Garrard, G.E., Bekessy, S.A., Mills, M., Camilleri, A.R., Fidler, F., Fielding, K.S., Gordon, A., Gregg, E.A., Kusmanoff, A.M., et al. (2019). Messaging matters: A systematic review of the conservation messaging literature. Biological Conservation *236*, 92–99. https://doi.org/10.1016/j.biocon.2019.05.020.

161. Kusmanoff, A.M., Fidler, F., Gordon, A., Garrard, G.E., and Bekessy, S.A. (2020). Five lessons to guide more effective biodiversity conservation message framing. Conservation Biology *34*, 1131–1141. https://doi.org/10.1111/cobi.13482.

162. Dean, A.J., and Wilson, K.A. (2023). Relationships between hope, optimism, and conservation engagement. Conservation Biology *37*, e14009. https://doi.org/10.1111/cobi.14020.

163. Jacobson, S.K., Morales, N.A., Chen, B., Soodeen, R., Moulton, M.P., and Jain, E. (2019). Love or Loss: Effective message framing to promote environmental conservation. Applied Environmental Education & Communication *18*, 252–265. https://doi.org/10.1080/1533015X.2018.1456380.

164. McAfee, D., Doubleday, Z.A., Geiger, N., and Connell, S.D. (2019). Everyone Loves a Success Story: Optimism Inspires Conservation Engagement. BioScience *69*, 274–281. https://doi.org/10.1093/biosci/biz019.

165. Hare, D., Dickman, A.J., Johnson, P.J., Rono, B.J., Mutinhima, Y., Sutherland, C., Kulunge, S., Sibanda, L., Mandoloma, L., and Kimaili, D. (2024). Public perceptions of trophy hunting are pragmatic, not dogmatic. Proc. R. Soc. B. *291*, 20231638. https://doi.org/10.1098/rspb.2023.1638.

166. Mathiesen, K.E., Barmoen, M., Bærum, K.M., and Johansson, M. (2022). Trust in researchers and researchers’ statements in large carnivore conservation. People and Nature *4*, 260–273. https://doi.org/10.1002/pan3.10282.

167. Sauer, K.A., Capps, D.K., Jackson, D.F., and Capps, K.A. (2021). Six minutes to promote change: People, not facts, alter students’ perceptions on climate change. Ecology and Evolution *11*, 5790–5802. https://doi.org/10.1002/ece3.7553.

168. Lang, K., and Spitzer, A.K.-L. (2020). How Discrimination and Bias Shape Outcomes. The Future of Children *30*, 165–186. https://doi.org/10.1353/foc.2020.0007.

169. Meyers, M., and Leide, J. (2020). Gender, Race, and the News: Enduring Bias. In The International Encyclopedia of Gender, Media, and Communication (John Wiley & Sons).

170. Boling, K.S., and Walker, D. (2021). How Race and Gender Impact the Perceived Objectivity of Broadcast Women of Color on Twitter. Social Media + Society *7*, 205630512110629. https://doi.org/10.1177/20563051211062921.

171. Abidin, C., Brockington, D., Goodman, M.K., Mostafanezhad, M., and Richey, L.A. (2020). The Tropes of Celebrity Environmentalism. Annu. Rev. Environ. Resour. *45*, 387–410. https://doi.org/10.1146/annurev-environ-012320-081703.

172. Brockington, D. (2009). Celebrity and the Environment: Fame, Wealth and Power in Conservation (Zed Books Ltd).

173. Taylor, D.E. (2014). The State of Diversity in Environmental Organizations. Green 2.0, 1–5. https://doi.org/10.13140/RG.2.2.32834.68804.

174. Taylor, D.E. (2015). Gender and Racial Diversity in Environmental Organizations: Uneven Accomplishments and Cause for Concern. Environmental Justice *8*, 165–180. https://doi.org/10.1089/env.2015.0018.

175. Miriti, M.N., Bailey, K., Halsey, S.J., and Harris, N.C. (2019). Hidden figures in ecology and evolution. Nature Ecology & Evolution *14249*, 14249. https://doi.org/10.1038/s41559-020-1270-y.

176. Schell, C.J., Guy, C., Shelton, D.S., Campbell-Staton, S.C., Sealey, B.A., Lee, D.N., and Harris, N.C. (2020). Recreating Wakanda by promoting Black excellence in ecology and evolution. Nature Ecology and Evolution. https://doi.org/10.1038/s41559-020-1266-7.

177. Chaudhury, A., and Colla, S. (2020). Next steps in dismantling discrimination: Lessons from ecology and conservation science. Conservation Letters, e12774. https://doi.org/10.1111/conl.12774.

178. Tseng, M., El-Sabaawi, R.W., Kantar, M.B., Pantel, J.H., Srivastava, D.S., and Ware, J.L. (2020). Strategies and support for Black, Indigenous, and people of colour in ecology and evolutionary biology. Nature Ecology and Evolution. https://doi.org/10.1038/s41559-020-1252-0.

179. Ashley-Smith, J. (2016). Losing the edge: the risk of a decline in practical conservation skills. Journal of the Institute of Conservation *39*.

180. Fernández-Llamazares, Á., Lepofsky, D., Lertzman, K., Armstrong, C.G., Brondizio, E.S., Gavin, M.C., Lyver, P.O., Nicholas, G.P., Pascua, P., Reo, N.J., et al. (2021). Scientists' Warning to Humanity on Threats to Indigenous and Local Knowledge Systems. Journal of Ethnobiology *41*, 144–169. https://doi.org/10.2993/0278-0771-41.2.144.

181. Malmer, P., Vanessa, M., Austin, B., and Tengö, M. (2020). Mobilisation of indigenous and local knowledge as a source of useable evidence for conservation partnerships. In Conservation Research, Policy and Practice, W. J. Sutherland, P. N. M. Brotherton, Z. G. Davies, N. Ockendon, N. Pettorelli, and J. A. Vickery, eds. (Cambridge University Press), pp. 82–113. https://doi.org/10.1017/9781108638210.006.

182. Haelewaters, D., Hofmann, T.A., and Romero-Olivares, A.L. (2021). Ten simple rules for Global North researchers to stop perpetuating helicopter research in the Global South. PLOS COMPUTATIONAL BIOLOGY.

183. Morales, N., Bisbee O'Connell, K., McNulty, S., Berkowitz, A., Bowser, G., Giamellaro, M., and Miriti, M.N. (2020). Promoting inclusion in ecological field experiences: Examining and overcoming barriers to a professional rite of passage. Bulletin Ecologic Soc America *101*, e01742. https://doi.org/10.1002/bes2.1742.

184. Fournier, A.M.V., and Bond, A.L. (2015). Volunteer field technicians are bad for wildlife ecology: Volunteer Field Technicians Are Bad for Wildlife Ecology. Wildl. Soc. Bull. *39*, 819–821. https://doi.org/10.1002/wsb.603.

185. Schusler, T.M., Espedido, C.B., Rivera, B.K., Hernández, M., Howerton, A.M., Sepp, K., Engel, M.D., Marcos, J., and Chaudhary, V.B. (2021). Students of colour views on racial equity in environmental sustainability. Nat Sustain *4*, 975–982. https://doi.org/10.1038/s41893-021-00759-7.

186. Matheka, D., Nderitu, J., Mutonga, D., Otiti, M., Siegel, K., and Demaio, A. (2014). Open access: academic publishing and its implications for knowledge equity in Kenya. Global Health *10*, 26. https://doi.org/10.1186/1744-8603-10-26.

187. Yoh, N., Holle, M.J.M., Willis, J., Rudd, L.F., Fraser, I.M., and Veríssimo, D. (2024). Understanding Author Choices in the Current Conservation Publishing Landscape. Conservation Biology.

188. Raby, C.L., and Madden, J.R. (2021). Moving academic conferences online: Aids and barriers to delegate participation. Ecology and Evolution *11*, 3646–3655. https://doi.org/10.1002/ece3.7376.

189. Wilson, J.W., and Biggs, D. (2016). Passport power: Entrenching inequality. Science *353*, 1216–1216. https://doi.org/10.1126/science.aajl1604.

190. Berger-Tal, O., and Saltz, D. (2016). Conservation behavior: applying behavioral ecology to wildlife conservation and management. (Cambridge University Press).

191. Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P., and Saltz, D. (2011). Integrating animal behavior and conservation biology: A conceptual framework. Behavioral Ecology *22*, 236–239. https://doi.org/10.1093/beheco/arq224.

192. Abrahms, B., Carter, N.H., Clark-Wolf, T.J., Gaynor, K.M., Johansson, E., McInturff, A., Nisi, A.C., Rafiq, K., and West, L. (2023). Climate change as a global amplifier of human–wildlife conflict. Nat. Clim. Chang. *13*, 224–234. https://doi.org/10.1038/s41558-023-01608-5.

193. Knowlton, J.L., and Graham, C.H. (2010). Using behavioral landscape ecology to predict species' responses to land-use and climate change. Biological Conservation *143*, 1342–1354. https://doi.org/10.1016/j.biocon.2010.03.011.

194. Sepúlveda, M.A., Bartheld, J.L., Monsalve, R., Gómez, V., and Medina-Vogel, G. (2007). Habitat use and spatial behaviour of the endangered Southern river otter (Lontra provocax) in riparian habitats of Chile: Conservation implications. Biological Conservation *140*, 329–338. https://doi.org/10.1016/j.biocon.2007.08.026.

195. Peters, N.M., Beale, C.M., Bracebridge, C., Mgumba, M.P., and Kendall, C.J. (2022). Combining models for animal tracking: Defining behavioural states to

understand space use for conservation. Journal of Biogeography *49*, 2016–2027. https://doi.org/10.1111/jbi.14483.

196. Villegas-Ríos, D., Jacoby, D.M.P., and Mourier, J. (2022). Social networks and the conservation of fish. Commun Biol *5*, 178. https://doi.org/10.1038/s42003-022-03138-w.

197. Hamede, Rodrigo.K., Bashford, J., McCallum, H., and Jones, M. (2009). Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecology Letters *12*.

198. Firth, J.A., Albery, G.F., Bouwhuis, S., Brent, L.J.N., and Salguero-Gómez, R. (2024). Understanding age and society using natural populations. Phil. Trans. R. Soc. B *379*, 20220469. https://doi.org/10.1098/rstb.2022.0469.

199. Caro, T. (1999). The behaviour–conservation interface. Trends in Ecology & Evolution *14*, 366–369. https://doi.org/10.1016/S0169-5347(99)01663-8.

200. Angeloni, L., Schlaepfer, M.A., Lawler, J.J., and Crooks, K.R. (2008). A reassessment of the interface between conservation and behaviour. Animal Behaviour *75*, 731–737. https://doi.org/10.1016/j.anbehav.2007.08.007.

201. Collins, A.C., Feuka, A.B., Nelson, J., Verahrami, A.K., and Bombaci, S. (2024). Perspectives on inclusion, safety, and belonging from members of the North American LGBTQIA+ conservation community. Conservation Biology *38*, e14389. https://doi.org/10.1111/cobi.14389.

202. Grinsted, L., Murgatroyd, C., and Burkett, J. (2024). Exploring attitudes to decolonising the science curriculum—A UK Higher Education case study. PLoS ONE *19*, e0312586. https://doi.org/10.1371/journal.pone.0312586.

203. Boyer, D. (2024). Infrastructural citizenship and geosolidarity. American Ethnologist *51*, 338–349.

204. Arts, B., Brockhaus, M., Giessen, L., and McDermott, C.L. (2024). The performance of global forest governance: Three contrasting perspectives. Forest Policy and Economics *161*, 103165. https://doi.org/10.1016/j.forpol.2024.103165.

205. De Vos, A., Cambronero-Solano, S., Mangubhai, S., Nefdt, L., Woodall, L.C., and Stefanoudis, P.V. (2023). Towards equity and justice in ocean sciences. npj Ocean Sustain *2*, 25. https://doi.org/10.1038/s44183-023-00028-4.

Report

Current Biology

# Sex-specific social aging in wild African lions

## Highlights

- Evidence of sex-modulated social aging in a wild lion population over 30 years
- Female connectivity declines with age, while average group size increases
- Male connectivity peaks in mid-life to males but dips in mid-life to females
- Connectivity is key to female longevity but associate numbers are key for males

## Authors

Lauren F. Rudd, Craig Packer,
Dora Biro, Josh A. Firth,
Gregory F. Albery

## Correspondence

lauren.rudd@gtc.ox.ac.uk

## In brief

Rudd et al. report sex-modulated social aging in wild lions. Female intra-sex connectivity declines with age, while male intra-sex connectivity dips in mid-life. Average group size increases with age in both sexes. Moreover, the quality of social associations is key to female longevity, while the quantity of associates is important for males.

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Report

# Sex-specific social aging in wild African lions

Lauren F. Rudd,[1,7,8,*] Craig Packer,[2] Dora Biro,[3] Josh A. Firth,[1,4] and Gregory F. Albery[5,6]
[1]Department of Biology, University of Oxford, Oxford OX1 3SZ, UK
[2]Department of Ecology, Evolution and Behaviour, University of Minnesota, St. Paul, MN 55108, USA
[3]Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY 14627, USA
[4]School of Biology, University of Leeds, Leeds LS2 9JT, UK
[5]Department of Biology, Georgetown University, Washington, DC 20057, USA
[6]Trinity College Dublin, Dublin D02 PN40, Republic of Ireland
[7]X (formerly Twitter): @laurenrudd18
[8]Lead contact
*Correspondence: lauren.rudd@gtc.ox.ac.uk
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## SUMMARY

There is a growing interest in social behavior change with age,[1–5] and the impacts of sociality on longevity,[6–8] but current knowledge is broadly limited to primates, societies structured by dominance hierarchies, or single-sex studies. It is less clear how social aging patterns emerge in carnivores. The African lion (*Panthera leo*), a species that lives in egalitarian fission-fusion societies, presents an exceptional opportunity to examine social aging. Across felids, lions are unique in their dependence on conspecifics for many essential processes,[9–11] and there is vast knowledge of lion behavioral ecology,[10–14] including documented reproductive senescence in both sexes.[14,15] Applying spatial-social network analyses across 30 years of data on the wild Serengeti lion population, we show that sex strongly modulates patterns of social aging and longevity. Group size increased with age for both sexes, but only males experienced significant changes in associate numbers (degree), specifically to females, which peaked in mid-life before declining. While aging females experienced declines in intra-sex connectivity (strength) and bond strength (mean strength), they peaked in both to males during mid-life. Male inter-sex strength also peaked in mid-life, while conversely their intra-sex strength and mean strength significantly dipped in mid-life. Although social associations were important for survival in both sexes, the investment diverged significantly: females' overall network connectivity was key for longevity, while the number of associates was important for males. These findings illustrate important potential effects of social aging in a wild carnivore and demonstrate how these diverge strongly between the sexes.

## RESULTS

Understanding how individuals' social behavior changes with age (referred to as "social aging") can help illuminate the role of aging individuals in structuring societies[1–5] and in processes such as disease transmission and information spread.[2,16,17] Multiple social aging hypotheses have been proposed, including within-individual changes (e.g., competition avoidance and alteration of spatial behavior) and population-level changes (e.g., selective disappearance and demographic shifts).[3] Throughout adulthood, inter-individual variation in social behavior is common and often emerges between the sexes.[18] As such, important between-sex differences in social aging are likely but remain understudied. Understanding sex-based variation could provide insights into drivers of social aging in wild populations and highlight the underlying evolutionary and ecological mechanisms.

Additionally, inter-individual variation in social behavior across the lifespan has been found to impact longevity variably across species.[6,8,19] Such phenomena are increasingly well documented, particularly in primates,[4–7] but are often restricted to a single sex.[3] Owing to the often-divergent social strategies of males and females,[20–23] lifetime sociality is likely to differentially impact fitness and longevity between the sexes.[24] As such, drawing broad inferences concerning the impact of sociality on longevity remains difficult, with findings often limited to particular taxa and single-sex examinations.[25] Particularly lacking are considerations of such processes in social carnivores. Owing to the unique ecological and evolutionary dynamics of such species, they may provide insights into the drivers and mechanisms of social aging that remain poorly understood.

The African lion (*Panthera leo*) is unique amongst felids: lions are highly social, with individuals living in egalitarian fission-fusion social groups.[11,14] Dispersal is highly sex skewed; most females remain with their natal pride (though some disperse to form new prides),[13] but all males disperse aged 2–4 and spend time in nomadic coalitions before taking residence in their first pride.[14,26] Coalitions can be resident within multiple prides at once, with larger coalitions more successful in retaining residencies and enjoying greater reproductive success.[27] Aging males exhibit reproductive senescence, likely due to their increasing vulnerability to intruding infanticidal males.[14] All female pride-mates breed at similar rates until reproductive senescence begins around ∼10 years old,[15] with cubs raised in creche groups where caring and nursing responsibilities are shared.[14,28,29] While individuals of both sexes spend significant time alone, essential behaviors (e.g., territorial defense, cub rearing, and hunting) are regularly executed in groups,[10,29] meaning singletons struggle to successfully reproduce and survive.[14,27] Despite the vast body of lion behavior research, little is known about intra-pride social associations, how sociality changes across a lifetime, and the role of sex-specific aging in mediating patterns of sociality. Given the variation in (and timing of) behaviors such as dispersal and reproduction between the sexes, we predict sex-based divergence in investment in the number of associates and strength of associations across the lifetime.

Using 30 years of data from 665 adult lions of the wild Serengeti population, we employed spatial and social network analyses to investigate sex-specific social aging and the association between fine-scale sociality and longevity. We compared individuals' (1) average group size, (2) number of associates (degree), (3) total sum amount of weighted social associations to others (strength), (4) social bond strength to associates (mean strength), and (5) the connectivity of their associates to one another (clustering) across their lifetimes within the population. Using an integrated nested Laplace approximation (INLA) model, we directly considered spatial autocorrelation in social network positions, accounting for each individual's average location at each timepoint. In addition, to decipher the effects of fine-scale, intra-pride social associations, we controlled for average annual group size as well as observation frequency, natal vs. foreign birth status, individual GPS collar status, year, current pride, natal pride, and individual identity. We analyzed male and female data separately to allow the comparison of sex-specific social aging and the impacts of sociality on longevity between sexes.

All models were substantially improved by considering spatial autocorrelation, indicating that social connectedness was spatially autocorrelated, so we report those models throughout. All response variables except male clustering showed at least a slight model improvement (DeltaDIC > 2), and the majority showed marked improvements (DeltaDIC > 100; Figure S1). However, accounting for these had little impact on other effect estimates, showing that spatial behavioral changes were unlikely to be driving the observed social aging trends.

## Female social aging and longevity

While average group size (average number of other individuals the focal lion was observed with per sighting) provides a simple measure of grouping behavior within a fission-fusion society, degree (number of unique individuals the focal lion was observed with over that year) provides an indication of overall gregariousness. Female lion networks were characterized by a substantial increase in group size with age (estimate 0.081; 95% CI 0.034, 0.127; $p < 0.001$; Figures 1 and 2). Once an individual's average group size was controlled for, we found no additional relationship between age and the unique number of associates females had (Figures 1 and 2).

The females' total sum of weighted social associations to other females (strength—a measure of an individual's overall social connectivity) decreased significantly with age (estimate −0.072; 95% CI −0.097, −0.048; $p < 0.001$; Figures 1 and 2). Aging studies commonly test for quadratic effects due to the possibility of non-linear relationships between response variables. A negative quadratic relationship with age was evident for females' strength to males, with a peak in connectivity during mid-life (estimate −0.067; 95% CI −0.091, −0.043; $p < 0.001$; Figures 1 and 2).

Female-female mean strength (a measure of the tightness of an individual's social bonds to its associates) declined with age (estimate −0.118; 95% CI −0.159, −0.078; $p < 0.001$), while female-male mean strength peaked significantly in mid-life (estimate −0.086; 95% CI −0.118, −0.054; $p < 0.001$; Figure 2).

The observed social aging trends contrasted strongly with the relationship between sociality and female longevity. Despite decreasing with age, female intra-sex strength was associated with greater longevity (estimate 0.039; 95% CI 0.012, 0.066; $p = 0.004$; Figures 1 and 3), confirming that the longevity effects cannot be attributed to selective disappearance. This was similarly true for the relationship between female-male strength and longevity (estimate 0.035, 95% CI 0.003, 0.068; $p = 0.030$; Figures 1 and 3). These results suggest that females benefit from investing in their social associations across their lifetime.

There was a small negative association between female-female clustering and longevity (estimate −0.063, CI −0.126, −0.001; $p = 0.047$). As such, there is potentially a survival cost to existing within tightly connected social cliques with female pride-mates, compared with groups with more fluid membership. Notably, there was no significant relationship between the number of associates females had (degree) and longevity (Figure 1).

## Male social aging and longevity

Similarly to females, there was a positive relationship between age and male average group size (estimate 0.172; 95% CI 0.064, 0.279; $p = 0.002$; Figures 1 and 2). Even when controlling for individuals' average group size, males also showed a strong and significant increase in their unique female associate numbers (degree) with age (estimate 0.172; 95% CI 0.087, 0.258; $p < 0.001$; Figures 1 and 2). There was a further negative quadratic effect of age, meaning the number of unique female associates peaked in mid-life (estimate −0.137, 95% CI −0.199, −0.075; $p < 0.001$; Figures 1 and 2). There was no significant change in the number of male-male associates with age (Figures 1 and 2).

Additionally, males showed decreasing strength with age when considering their intra-sex connections (estimate −0.321; 95% CI −0.399, −0.243; $p < 0.001$; Figure 1), but the quadratic relationship showed peaks in early and late-life (estimate 0.131; 95% CI 0.074, 0.187; $p < 0.001$; Figure 2). Male-female strength showed the opposite pattern, with a peak in mid-life (estimate −0.075; 95% CI −0.127, −0.024; $p = 0.004$; Figures 1 and 2).

As was true for females, male intra-sex mean strength decreased significantly with age (estimate −0.283; 95% CI −0.381, −0.184; $p < 0.001$; Figures 1 and 2). However, when considering the quadratic relationship, and in contrast to females, male-male mean strength peaked in early and late life (estimate 0.141; 95% CI 0.071, 0.211; $p < 0.001$; Figures 1 and 2).

Male longevity was significantly positively related to the number of male associates (estimate 0.087; 95% CI 0.002, 0.173; $p = 0.045$), and the number of female associates (estimate 0.134; 95% CI 0.046, 0.222; $p = 0.003$; Figures 1 and 3).

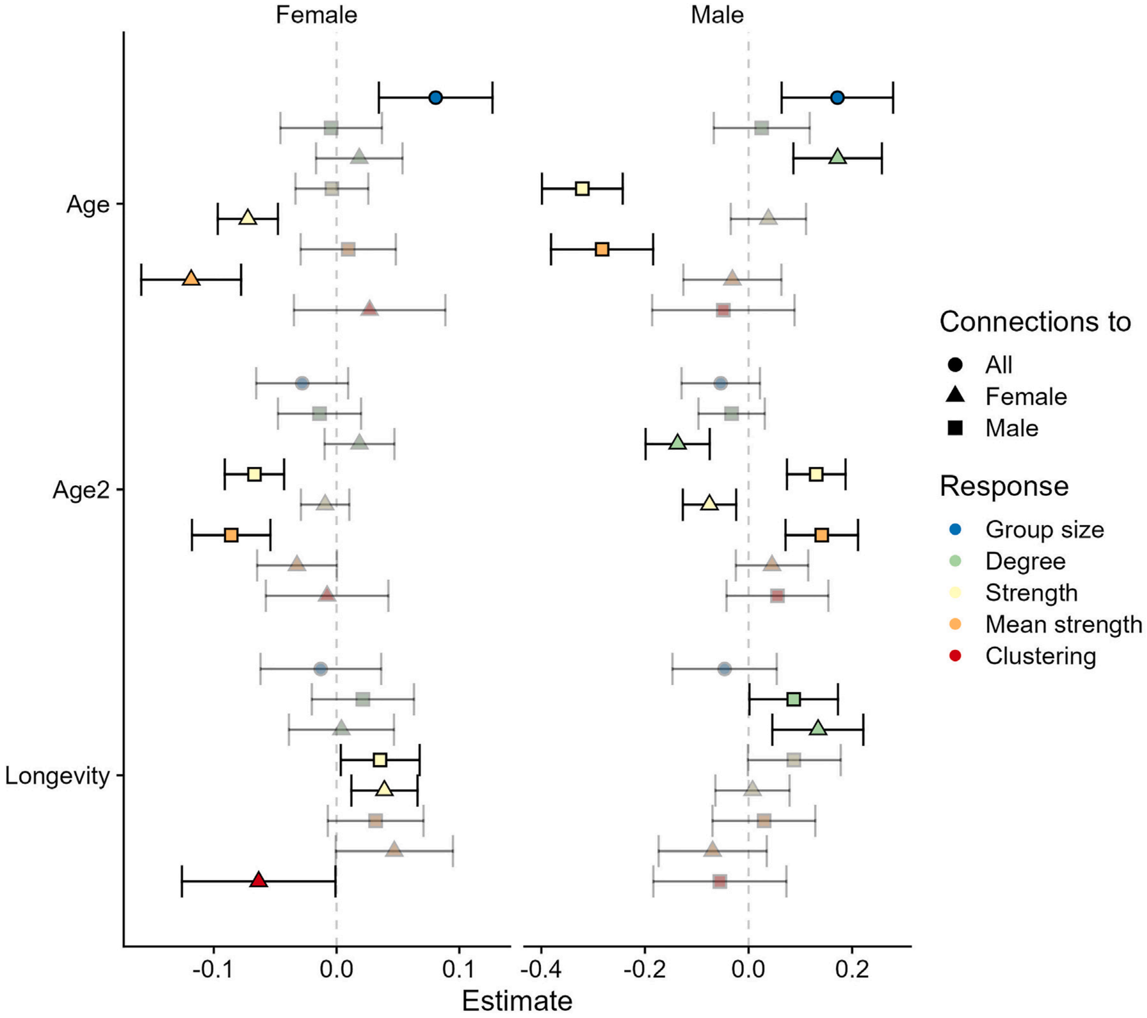

**Figure 1. Associations between age, longevity, and social metrics**

Estimates taken from the SPDE single-sex model for females (left) and males (right) showing the age and longevity effects for each social metric tested. Points represent the model estimate with error bars showing the 95% credibility intervals (estimated according to the 95% upper and lower quantiles of the posterior density distribution for each effect). Bold points indicate a significant relationship; faded points indicate a non-significant relationship. See also Figure S1 and Table S1.

## DISCUSSION

Our findings demonstrate strong, sex-dependent, and often-nonlinear changes in social behavior with age in a wild carnivore, the African lion. These relationships existed even after accounting for individuals' group size changes, and the metrics of fine-scale social behavior were also related to longevity. It is plausible that the strongly divergent patterns of sex-based social aging relate to the profound differences in reproductive biology and social behavior between males and females. Similar to the orthodoxy from studies of other mammals (e.g., primates and ungulates[2,3]), aging females appeared to broadly lose social connectivity while retaining a similar absolute number of associates. In contrast, males' connectivity was highly nonlinear and peaked in early and late life, showing that there are strongly divergent drivers governing the expression of social behavior. This illustrates social aging patterns should be considered more broadly in social animals, potentially uncovering a range of further processes governing the underlying causes and consequences of ecological and behavioral processes.[1,2] As theorized in primates specifically,[5] animals with highly divergent sex roles in their society may exhibit similar divergence in social aging patterns due to shifts in motivation and power; further comparative work may help to elucidate the wider drivers and consequences.

### Group size and number of associates

Due to the fission-fusion structure of lion society, individuals' group size and the total number of unique associates they are observed with (degree) provide two informative yet relatively simple social measures. There was a significant increase in female sub-group size with age but a lack of change in associate numbers (when controlling for group size changes). This could partly be explained by reproductive senescence,[15] as mothers

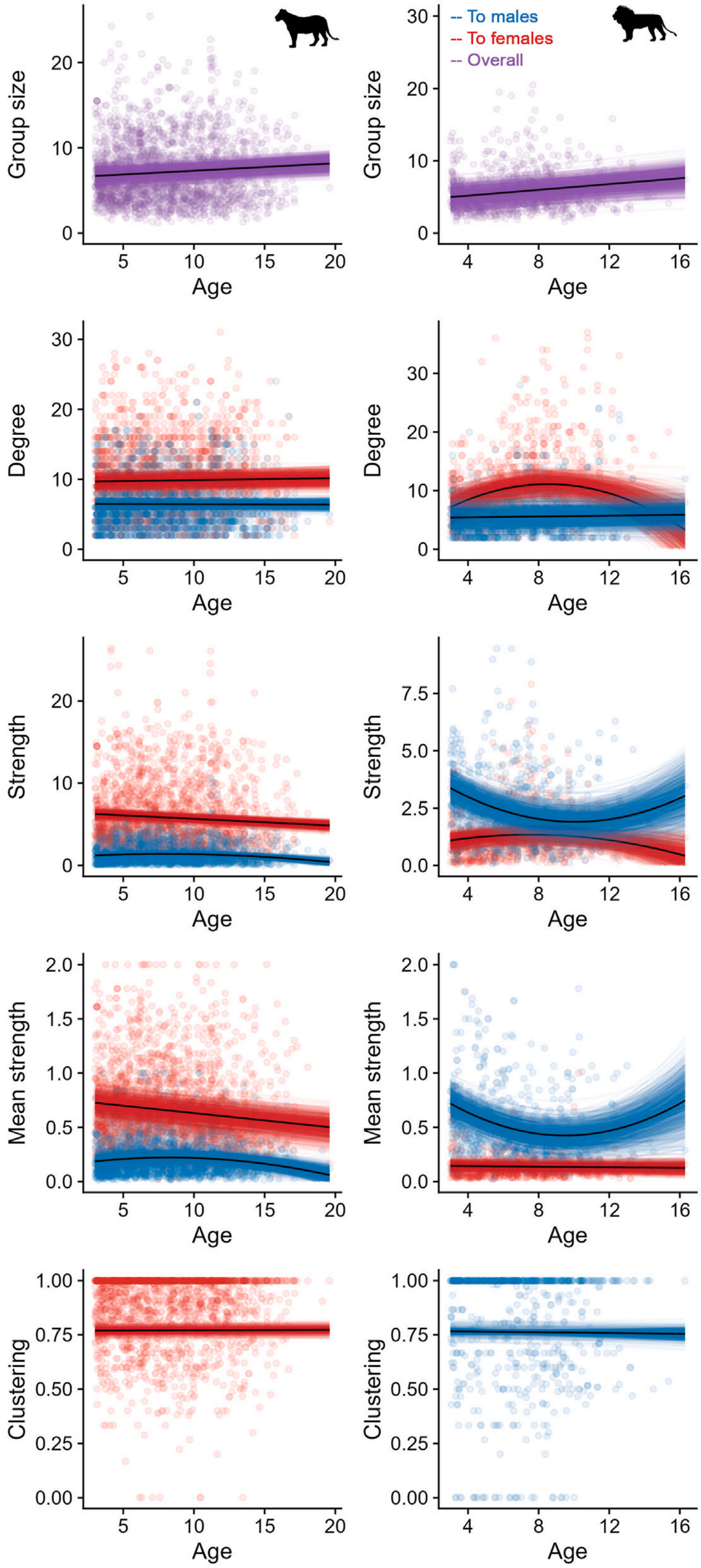

**Figure 2. Social aging patterns vary between the sexes**

Age related changes in (from top to bottom) group size, degree, strength, mean strength, and clustering for females (left column) and males (right column). Red points and lines indicate associations to females, blue points and lines indicate associations with males, and purple points and lines indicate associations to both sexes combined. Where significant, quadratic age effects are included in the plot, generating n- or u-shaped curves. The black lines represent the mean of the posterior distribution for the age effect estimate; the colored lines are 100 random draws from the posterior to represent uncertainty. The points represent individual-by-year replicates, with transparency to allow for visualization of overplotting. For females, group size, strength, and mean strength plots show significant relationships. For males, group size, degree (to females only), strength, and mean strength (to males only) plots show significant relationships. See also Figure S1 and Table S1.

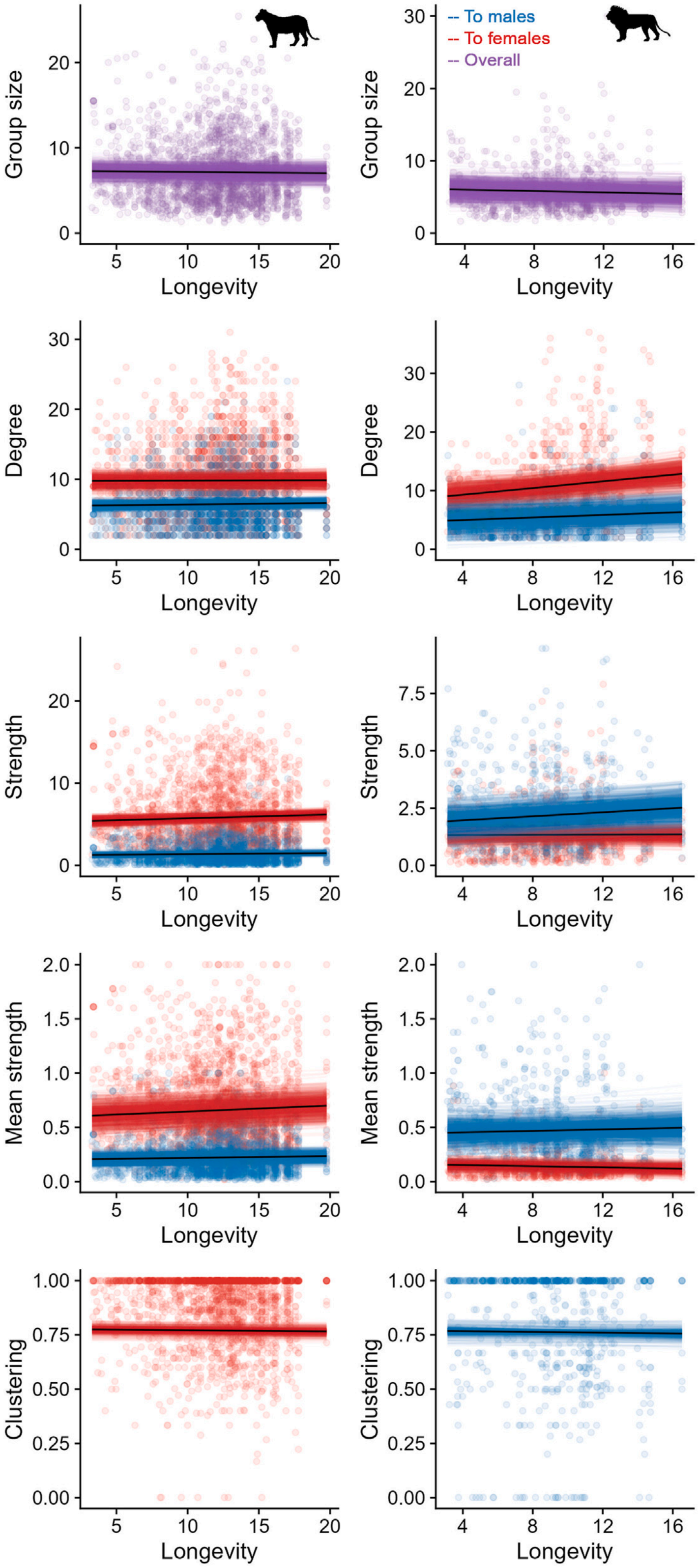

**Figure 3. Sociality correlates with longevity differentially between the sexes**

Longevity effects of (from top to bottom) group size, degree, mean strength, and clustering for females (left column) and males (right column). Red points indicate associations to females only, while blue points indicate associations with males only, and purple points and lines indicate associations to both sexes combined. The black lines represent the mean of the posterior distribution for the age effect estimate; the colored lines are 100 random draws from the posterior to represent uncertainty. The points represent individual-by-year replicates, with transparency to allow for visualization of overplotting. For females, strength and clustering plots show significant relationships. For males, the degree plot shows a significant relationship. See also Figure S1 and Table S1.

are highly dependent on small creche groups while cub rearing.[28,29] Furthermore, females frequently hunt alone or in substantially smaller groups than the maximum pride size.[14,29] In other social apex predators, declines in hunting success with age have been observed,[30] and aging female lions do show signs of deteriorating physicality that could impair their hunting ability. It is plausible that aging females become increasingly dependent on the pride for food, rather than hunting themselves, and so are observed more frequently in bigger group sizes. Understanding female hunting behavior across the lifespan could elucidate this further.

Similarly, male sub-group size increased with age, which could reflect the increasing likelihood of a male's pride being taken over by intruding males.[14] Further research into whether aging males spend an increasing proportion of their time with the bulk of the pride, in recognition of their physical vulnerability, would be useful. While female associate numbers did not change with age, males exhibited an increase in female associate numbers to a mid-life peak even when controlling for group size changes. This is likely because, in the Serengeti, many coalitions are resident within multiple prides simultaneously. These prides grow in size to a tipping point; however, pride residencies can also be surrendered by coalitions as they age, particularly if their non-dispersing daughters have reached reproductive maturity.[14]

Across the lifetime, neither yearly average group size nor yearly number of associates held statistically significant relationships with female longevity, suggesting that the extent of grouping behavior individuals display does not directly relate to survival. However, male longevity increased when their associate numbers were higher, and this was true when only considering their associations to females, or to other males. This could be partly indicative of selective disappearance[3] in that larger coalitions are more successful in maintaining pride residence, and therefore persisting in the study area, when compared to smaller coalitions.[14] Further, males resident within larger prides (or multiple prides) may simultaneously have access to better quality territory,[10] which would positively contribute to their survival.

## Connectivity and bond strength

Lions demonstrated significant reductions in their overall connectivity to same-sex individuals (intra-sex strength) and average bond strength to their associates (mean strength) with age. Sex-specific differences were again found: female lions exhibited a peak in both metrics in mid-life to males only. Males exhibited early- and late-life peaks in strength and mean strength when considering their male associates only. This contrasted with the evident mid-life peak in strength to females.

These findings may reflect the differing influence of reproductive behavior on social aging between the sexes. Females are reliant on the creche for cub rearing and protection from infanticidal males during their prime adult years.[31] As reproductive senescence progresses, investment in creche-mate associations may decrease. Additionally, the early-life peak in mean strength mirrors the time of highest vulnerability for females that do disperse,[14] so this could be when they are most dependent on their cohort for survival. For resident males, the biggest threat to their reproductive output is intruding male competitors. Counteracting this threat requires early-life investment in coalition bonds during the natal pride and nomadic life stages. These within-coalition bonds may once again become important as males age and become more vulnerable to intruding males.[13] Conversely, aging males' drop off in overall connectivity to females (male inter-sex strength) could reflect reproductive senescence and perhaps even post-pride residence social behavior when intra-sex associations will dominate.[14]

Across their lifetime, lionesses that invested more in their social associations (with greater intra- and inter-sex strength) appeared to live longer. The direct causal mechanisms underpinning this remain unclear; however, where similar patterns exist in primates, it has been hypothesized that females experience fitness benefits from their associates through increased buffering against stressful events[6] and improved cooperation in shared behaviors.[7] Both could tangibly impact female lion longevity given the threat frequently posed by infanticidal males, and the extensive cooperation required during territorial defense, hunting and cub rearing. Another possibility is that females are more likely to emigrate from the study area if they are less strongly connected to others, generating the perception that increased connectivity improves longevity.

## Cliquishness

For females, there was a slight but significant negative relationship between longevity and their embeddedness in highly clustered intra-sex groups (as opposed to groups with relatively frequently shifting membership). This may reflect the higher rate of fission-fusion in larger prides, which hold better quality territories.[10] Similarly, this suggests that a tendency for individuals to be overly cliquish (and less integrated in the wider population) holds relative costs, compared with being more socially transient and having connections outside of their immediate clique.

## Ecological consequences

These findings will have a range of ecological and evolutionary implications for age-structured lion societies. For example, lionesses' decrease in social connectedness could drive reduced exposure to pathogens, while males' tendency to gain extra unique associates might disproportionately predispose them to acquiring novel parasites.[16,32] Such changes in exposure rates could interact with their reproductive investment and resulting changes in immune resistance,[33] as well as with immunosenescence.[16] Given that this population has previously experienced high-mortality disease outbreaks,[34,35] understanding these phenomena could be important for predicting the resilience of the Serengeti lion population in the future. Similarly, there could be important consequences for social learning, as knowledge about the environment is likely to improve with age.[36] As such older lionesses are likely to be key resources for prides, but their tendency to become less connected could reduce the ability for information to spread. Yet more research into how behaviors spread socially in wild social networks with diverse structures is now needed.[37]

## Conclusion

We found evidence of sex-differentiated patterns of social aging, and links between lifetime sociality and longevity, in African lions. The individual-based and long-term nature of our data, as well as our incorporation of both age and longevity effects, confirm that age-related patterns of sociality likely emerge through a combination of within-individual aging and selective disappearance. Females lived longer when they were more strongly connected to their associates but existed in less tightly interconnected groups. This was true despite decreases in strength and mean strength with age. Additionally, we found that, despite interacting with the same number of individuals as they age, females are on average found in larger groups. These social aging patterns may mirror declines in reproductive output and so creche attendance,[11,15,28] as well as increasing reliance on pride hunts due to physical senescence. As males aged, their number and strength of connections to female associates increased to a mid-life peak. However, the strength and mean strength of their intra-sex connections to other males were highest in early and late life. Further, males with more associates appeared to live longer. These findings likely reflect changes in pride size and residency patterns with age, as prides grow but coalitions surrender secondary prides containing mature daughters.[14] Additionally, as males in larger coalitions are more likely to be resident in multiple prides, they may concurrently have access to better quality territories that will contribute positively to their fitness and survival.[10] Our results demonstrate social aging in wild lions, how this can shape individual longevity, and the role of sex in modulating this relationship. Such insights add to existing knowledge of the species' sociality and further our understanding of social aging across diverse mammalian systems.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.07.040.

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## AUTHOR CONTRIBUTIONS

Conceptualization, L.F.R., D.B., C.P., J.A.F., and G.F.A.; methodology, L.F.R., G.F.A., and J.A.F.; formal analysis, L.F.R. and G.F.A.; writing – original draft, L.F.R.; writing – review and editing, L.F.R., G.F.A., D.B., C.P., and J.A.F.; visualization, L.F.R. and G.F.A.; supervision, D.B., C.P., J.A.F., and G.F.A.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## REFERENCES

1. Woodman, J., Gokcekus, S., Beck, K., Green, J., Nussey, D., and Firth, J. (2024). The ecology of aging in wild societies: linking age structure and social behaviour in natural populations. Preprint at ecoevoRxiv. https://doi.org/10.32942/X21893.
2. Siracusa, E.R., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Social aging: exploring the drivers of late-life changes in social behaviour in mammals. Biol. Lett. *18*, 20210643. https://doi.org/10.1098/rsbl.2021.0643.
3. Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2022). Aging red deer alter their spatial behaviour and become less social. Nat. Ecol. Evol. *6*, 1231–1238. https://doi.org/10.1038/s41559-022-01817-9.
4. Machanda, Z.P., and Rosati, A.G. (2020). Shifting sociality during primate aging. Philos. Trans. R. Soc. Lond. B Biol. Sci. *375*, 20190620. https://doi.org/10.1098/rstb.2019.0620.
5. Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Emery Thompson, M., Muller, M.N., Wrangham, R.W., and Machanda, Z.P. (2020). Social selectivity in aging wild chimpanzees. Science *370*, 473–476. https://doi.org/10.1126/science.aaz9129.
6. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. Curr. Biol. *20*, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067.
7. Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M.L., and Brent, L.J.N. (2019). Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. Proc. Biol. Sci. *286*, 20191991. https://doi.org/10.1098/rspb.2019.1991.
8. Blumstein, D.T., Williams, D.M., Lim, A.N., Kroeger, S., and Martin, J.G.A. (2018). Strong social relationships are associated with decreased longevity in a facultatively social mammal. Proc. Biol. Sci. *285*, 20171934. https://doi.org/10.1098/rspb.2017.1934.
9. Scheel, D., and Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. Anim. Behav. *41*, 697–709. https://doi.org/10.1016/S0003-3472(05)80907-8.
10. Mosser, A., and Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, Panthera leo. Anim. Behav. *78*, 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024.
11. Packer, C., Pusey, A.E., and Eberly, L.E. (2001). Egalitarianism in female African lions. Science *293*, 690–693. https://doi.org/10.1126/science.1062320.
12. Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., and Sinclair, A.R.E. (2005). Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. Most *307*, 390–393.
13. VanderWaal, K.L., Mosser, A., and Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Anim. Behav. *77*, 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028.
14. Packer, C. (2023). The Lion: Behaviour, ecology and conservation of an iconic species (Princeton University Press).

15. Packer, C., Tatar, M., and Collins, A. (1998). Reproductive cessation in female mammals. Nature *392*, 807–811. https://doi.org/10.1038/33910.

16. Albery, G.F., Sweeny, A.R., and Webber, Q. (2023). How behavioural aging affects infectious disease. Neurosci. Biobehav. Rev. *155*, 105426. https://doi.org/10.1016/j.neubiorev.2023.105426.

17. Bourke, A.F.G. (2007). Kin Selection and the Evolutionary Theory of Aging. Annu. Rev. Ecol. Evol. Syst. *38*, 103–128. https://doi.org/10.1146/annurev.ecolsys.38.091206.095528.

18. Delmé, C., Jackson, N., Class, B., Strickland, K., Potvin, D.A., and Frère, C.H. (2023). Adaptive significance of affiliative behaviour differs between sexes in a wild reptile population. Proc. Biol. Sci. *290*, 20230805. https://doi.org/10.1098/rspb.2023.0805.

19. Barocas, A., Ilany, A., Koren, L., Kam, M., and Geffen, E. (2011). Variance in Centrality within Rock Hyrax Social Networks Predicts Adult Longevity. PLoS One *6*, e22375. https://doi.org/10.1371/journal.pone.0022375.

20. Clutton-Brock, T.H., and Huchard, E. (2013). Social competition and selection in males and females. Philos. Trans. R. Soc. Lond. B Biol. Sci. *368*, 20130074. https://doi.org/10.1098/rstb.2013.0074.

21. Kulik, L., Amici, F., Langos, D., and Widdig, A. (2015). Sex Differences in the Development of Social Relationships in Rhesus Macaques (Macaca mulatta). Int. J. Primatol. *36*, 353–376. https://doi.org/10.1007/s10764-015-9826-4.

22. Gibson, Q.A., and Mann, J. (2008). Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. Anim. Behav. *76*, 375–387. https://doi.org/10.1016/j.anbehav.2008.01.021.

23. Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., Langergraber, K.E., Zuberbühler, K., Wittig, R.M., and Mundry, R. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. R. Soc. Open Sci. *4*, 161081. https://doi.org/10.1098/rsos.161081.

24. Tidière, M., Gaillard, J.-M., Müller, D.W.H., Lackey, L.B., Gimenez, O., Clauss, M., and Lemaître, J.-F. (2015). Does sexual selection shape sex differences in longevity and senescence patterns across vertebrates? A review and new insights from captive ruminants: sexual selection and senescence. Evolution *69*, 3123–3140. https://doi.org/10.1111/evo.12801.

25. Campos, F.A., Villavicencio, F., Archie, E.A., Colchero, F., and Alberts, S.C. (2020). Social bonds, social status and survival in wild baboons: a tale of two sexes. Philos. Trans. R. Soc. Lond. B Biol. Sci. *375*, 20190621. https://doi.org/10.1098/rstb.2019.0621.

26. Pusey, A.E., and Packer, C. (1987). The Evolution of Sex-Biased Dispersal in Lions. Beyond Behav. *101*, 275–310. https://doi.org/10.1163/156853987X00026.

27. Bygott, J.D., Bertram, B.C.R., and Hanby, J.P. (1979). Male lions in large coalitions gain reproductive advantages. Nature *282*, 839–841. https://doi.org/10.1038/282839a0.

28. Pusey, A.E., and Packer, C. (1994). Non-offspring nursing in social carnivores: Minimizing the costs. Behav. Ecol. *5*, 362–374. https://doi.org/10.1093/beheco/5.4.362.

29. Packer, C., Scheel, D., and Pusey, A.E. (1990). Why Lions Form Groups: Food is Not Enough. Am. Nat. *136*, 1–19.

30. MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R., and Packer, C. (2009). Predatory senescence in aging wolves. Ecol. Lett. *12*, 1347–1356. https://doi.org/10.1111/j.1461-0248.2009.01385.x.

31. Packer, C., and Pusey, A.E. (1983). Adaptations of Female Lions to Infanticide by Incoming Males. Am. Nat. *121*, 716–728.

32. Siracusa, E.R., Pavez-Fox, M.A., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Snyder-Mackler, N., Higham, J.P., Brent, L.J.N., and Silk, M.J. (2024). Social aging can protect against infectious disease in a group-living primate. Preprint at bioRxiv. https://doi.org/10.1101/2024.03.09.584237.

33. Neggazi, S.A., Noreikiene, K., Öst, M., and Jaatinen, K. (2016). Reproductive investment is connected to innate immunity in a long-lived animal. Oecologia *182*, 347–356. https://doi.org/10.1007/s00442-016-3657-7.

34. Munson, L., Terio, K.A., Kock, R., Mlengeya, T., Roelke, M.E., Dubovi, E., Summers, B., Sinclair, A.R.E., and Packer, C. (2008). Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. PLoS One *3*, e2545. https://doi.org/10.1371/journal.pone.0002545.

35. Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofman-Lehmann, R., Lutz, H., et al. (1996). A canine distemper virus epidemic in Serengeti lions (Panthera leo). Nature *379*, 441–445. https://doi.org/10.1038/379441a0.

36. McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J., and Moss, C. (2011). Leadership in elephants: the adaptive value of age. Proc. Biol. Sci. *278*, 3270–3276. https://doi.org/10.1098/rspb.2011.0168.

37. Firth, J.A. (2020). Considering Complexity: Animal Social Networks and Behavioural Contagions. Trends Ecol. Evol. *35*, 100–104. https://doi.org/10.1016/j.tree.2019.10.009.

38. Franks, D.W., Ruxton, G.D., and James, R. (2010). Sampling animal association networks with the gambit of the group. Behav. Ecol. Sociobiol. *64*, 493–503. https://doi.org/10.1007/s00265-009-0865-8.

39. Farine, D.R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. *84*, 1144–1163. https://doi.org/10.1111/1365-2656.12418.

40. Van De Pol, M., and Verhulst, S. (2006). Age-Dependent Traits: A New Statistical Model to Separate Within- and Between-Individual Effects. Am. Nat. *167*, 766–773. https://doi.org/10.1086/503331.

## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Data | Github | https://github.com/gfalbery/Old_Lion. |
| Software and algorithms | | |
| R code | Github | https://github.com/gfalbery/Old_Lion. |

### RESOURCE AVAILABILITY

### Lead contact

Further information and requests for resources relating to this manuscript should be directed to and will be fulfilled by Lauren Rudd (lauren.rudd@gtc.ox.ac.uk).

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

- Data have been deposited (see key resources table) and are available as of the date of publication.
- All original code has been deposited (see key resources table) and is available as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

### EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

This study did not use experimental model animals, experimental *in vivo* animals, human participants, plants, microbe strains, cell lines, or primary cell cultures.

### Study system

The research was carried out using data from the long-term study of African lions in the Serengeti National Park, Tanzania. The study area comprised 2700km$^2$ of the national park, including both the grassland plains and acacia woodlands habitats. Two seasons can be identified, with the wet season spanning November-May and the dry season spanning June-October. Year-round prey densities are higher in the woodlands habitat (which is more heterogeneous), while in the plains habitat prey density fluctuates with seasonal migrations (and is considerably lower in the dry season).[12]

Throughout the study area, female lions generally live in fission-fusion prides composed of related female adults and their offspring. Pride size ranges from 2 to 20 individuals, and 75% of female offspring cohorts are recruited back into the mothers' pride, while 25% disperse to form new prides (often in adjacent territories).[14] Conversely, male offspring disperse from the natal pride and form coalitions of up to 9 individuals, composed of kin and non-kin. These coalitions live a nomadic life following dispersal until they are able to take over a pride of their own, usually between age 2-4.[14,27] There is no clear dominance hierarchy among female pride-mates[10] or male coalition-mates.[14]

### Data collection

The observational data used in this study was collected between 1984 and 2013. During this time, 1 female per pride was fitted with a GPS collar and was tracked at least once every 2 weeks. Once located, individuals within 200m of each other were considered co-occurring, so recorded as part of the same group sighting event (GPS location, date and time). Opportunistic sightings of non-collared individuals and groups were recorded in the same way. For each known individual (recognized by facial markings), age (estimated from date of first sighting as a cub or adult, accurate to within 2-3 weeks and 1 year respectively), sex, natal pride (if born in the study site) and current pride data was available.

Method details

### Social metrics and networks

Only data on individuals aged 3 and above were included, giving a total of 150842 observations of 665 individuals (mean per individual [SD] = 48.1 [85.2]) from 60 prides over 30 years. We created social networks at yearly intervals commencing in June 1984, following the seasonal calendar, running from the start of the dry season to the end of the wet season. Following the "gambit of the group" approach,[38] individuals observed in the same group according to the date and GPS location recorded (as described in the "Data collection" section above) were classed as associating at that time-point. This process generated a "group-by-individual" matrix, and the Simple Ratio Index (SRI) was used for deriving dyadic association matrices (i.e., social networks) between individuals, where the proportion of overall sightings in which two individuals were observed together was calculated rather than the absolute count (see Farine and Whitehead[39] for more details). All SRI values range between 0 (individuals never seen together) and 1 (individuals always seen together).

Using the annual networks, we derived 5 commonly used metrics to characterize lion social behavior.

(1) Group size: the average number of other individuals the focal lion was observed with per sighting
(2) Degree: the number of unique individuals the focal lion was observed with over the course of the year (i.e., number of the node's network edges)
(3) Strength: the total weighted sum of the focal lion's associations within the network over the course of the year (i.e., sum of the node's weighted edges, thereby quantifying overall connectivity)
(4) Mean strength: the average value of the focal lion's weighted associations to its non-zero associates over the course of the year (i.e., mean of the node's weighted edges, thereby quantifying bond strength)
(5) Clustering: the propensity for a focal individual's associates to also be associated with one another (with higher values indicating greater "cliquishness")

## Statistical analysis

We fitted linear models using the Integrated Nested Laplace Approximation (INLA), which is a deterministic Bayesian modelling framework. We fitted three broad classes of models: those examining the population as a whole, only females, or only males. We only included individuals aged 3 and above. This analytical setup is based on an established method for differentiating within- and between-individual age effects[40] which we have used in social aging models before[3] : by fitting age, longevity, and individual identity, the model controls for selective disappearance of certain individuals (i.e., of the more or less social) through mortality. This allows us to identify whether age-related changes in social network position are resulting from within-individual behavioural aging, or whether such patterns might emerge through population-level structural changes.

As such, each model included the following fixed explanatory variables: age (continuous, in years); Age$^2$ to detect quadratic shapes (continuous, centred around the mean value for age); Longevity (continuous, calculated as age at disappearance from study site in years; Observations (continuous, calculated as the number of times an individual was seen that year); Group size (continuous, calculated as an annual mean from the observation data); Foreign (binary variable, representing whether or not the individual was born in the study area); and Collared (binary variable, representing whether or not they had a GPS collar). We also included a suite of random effect factors: Natal pride (the pride in which an individual was born); Pride (the pride in which an individual was most often seen each year); Year; and Individual identity. We did not fit a Maximum Pride Size factor in addition to the Group Size and Pride based on the comparable results of prior analyses (see Figure S2 for SPDE model including Max Pride Size; Figure S3 for correlation between Max Pride Size and Group Size). In the overall models, we also fitted some effects to examine differences between sexes: first a main sex effect, and then interactions between sex and our continuous variables (Age, Age$^2$, Longevity, Observations, and Group size).

INLA models allow the fitting of a stochastic partial differentiation equation (SPDE) effect to account for spatiotemporal autocorrelation. Controlling for spatial autocorrelation is potentially important because in this and other wildlife populations, older individuals could exhibit changes in spatial behaviour that drive changes in social behaviour.[3,16] Further, spatial patterns of environmental structure or demography could drive social changes across the study area in a way that confounds with age structuring.[1] As such, isolating the spatial and social components of behavioural aging patterns is therefore likely to be important for ecological understanding.

To investigate spatial dependence in this way, we used each individual's average X and Y coordinate in each year (i.e., their annual spatial centroid); the effect modelled the expectation that individuals will have more similar response values (i.e., social network positions) when their locations were closer in space. To assess whether the models were significantly spatially autocorrelated, we first fitted the base model, and then added the SPDE effect and compared the model fit using deviance information criterion (DIC). We took 5 DIC to differentiate between competitive models, such that if the SPDE effect reduced DIC by more than 5 it was taken to be significantly autocorrelated. The base model + SPDE effect estimates for each of the single sex models can be found in Table S1, and the spatial DIC changes can be seen in Figure S1.

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# Supplemental Information

# Sex-specific social aging in wild African lions

**Lauren F. Rudd, Craig Packer, Dora Biro, Josh A. Firth, and Gregory F. Albery**

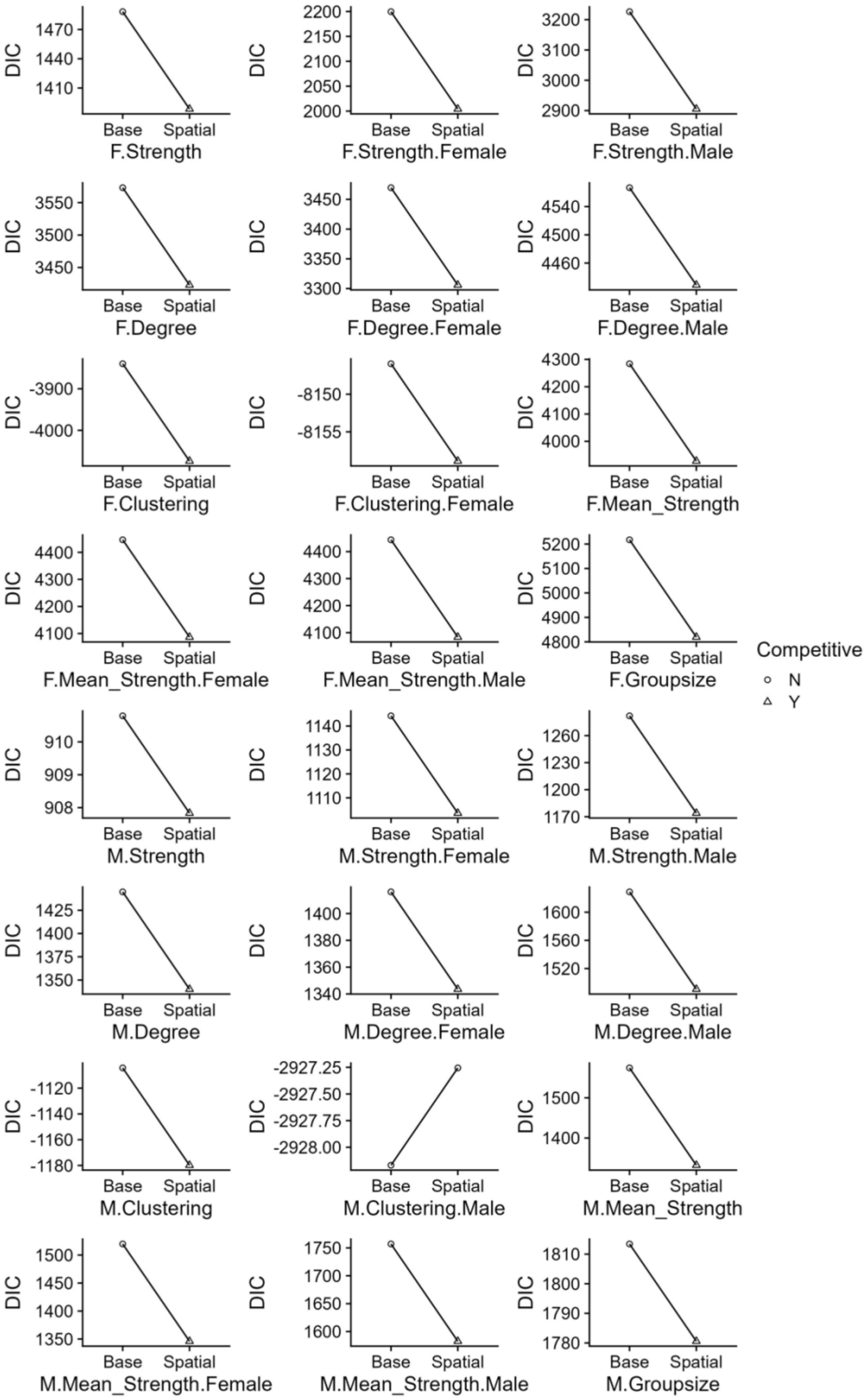


**Figure S1. Spatial DIC Changes, Related to Figure 1, Figure 2, Figure 3 and STAR Methods.** DIC changes associated with fitting a spatial autocorrelation effect in our INLA models. More negative changes denote better-fitting models, and therefore more spatially autocorrelated social networks.

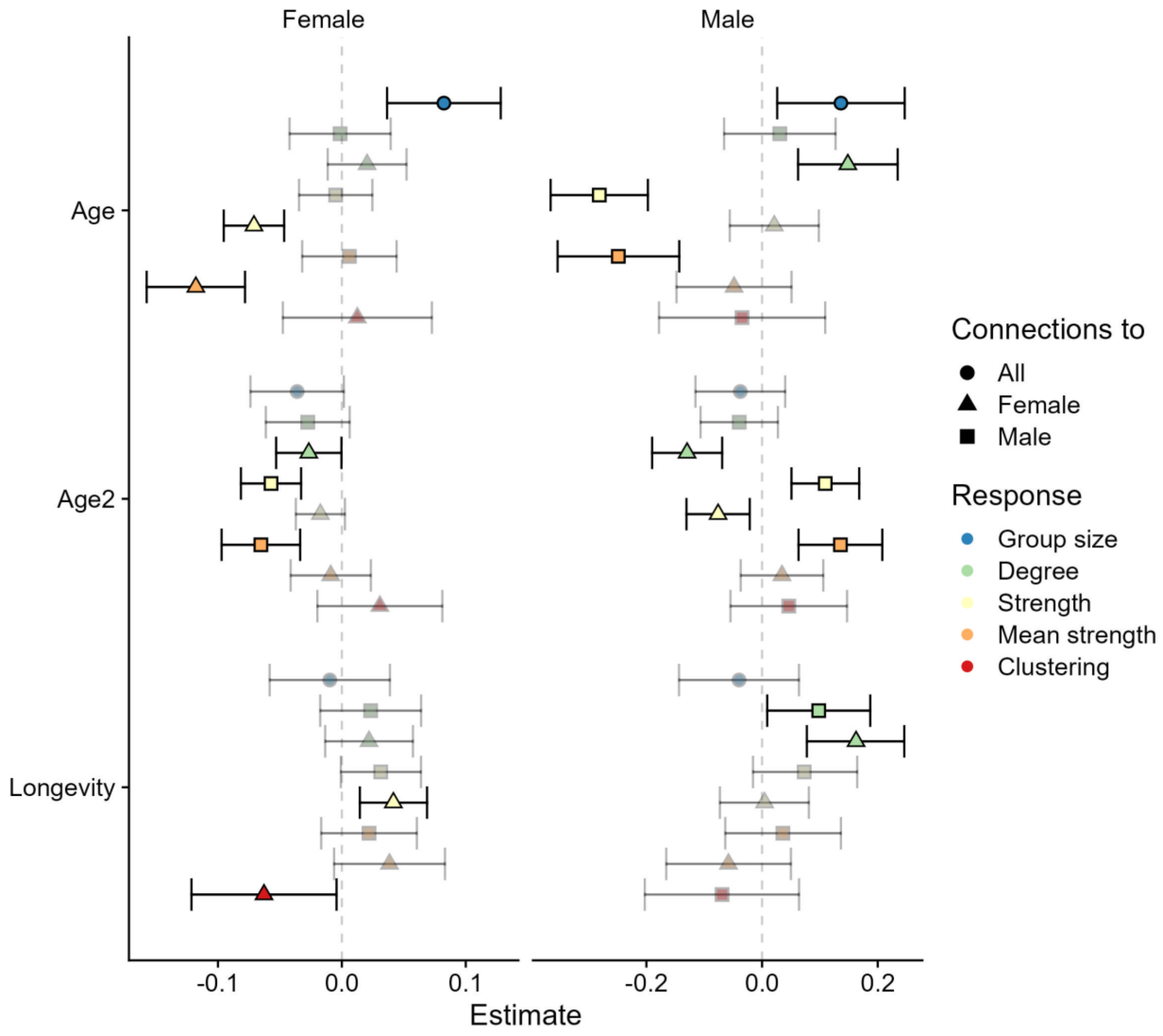


**Figure S2. Associations between age, longevity and social metrics for the SPDE model including max pride size, Related to STAR Methods.** Estimates taken from the single sex model for females (left) and males (right), showing the age and longevity effects for each social metric tested. Points represent the model estimate with error bars showing the 95% CI. Bold points indicate a significant relationship, faded points indicate a non-significant relationship. The model output is largely comparable to that included in the main results despite the addition of max pride size. There is an additional negative quadratic effect of age on female-female degree, and a loss of the positive female-male strength effect on longevity.

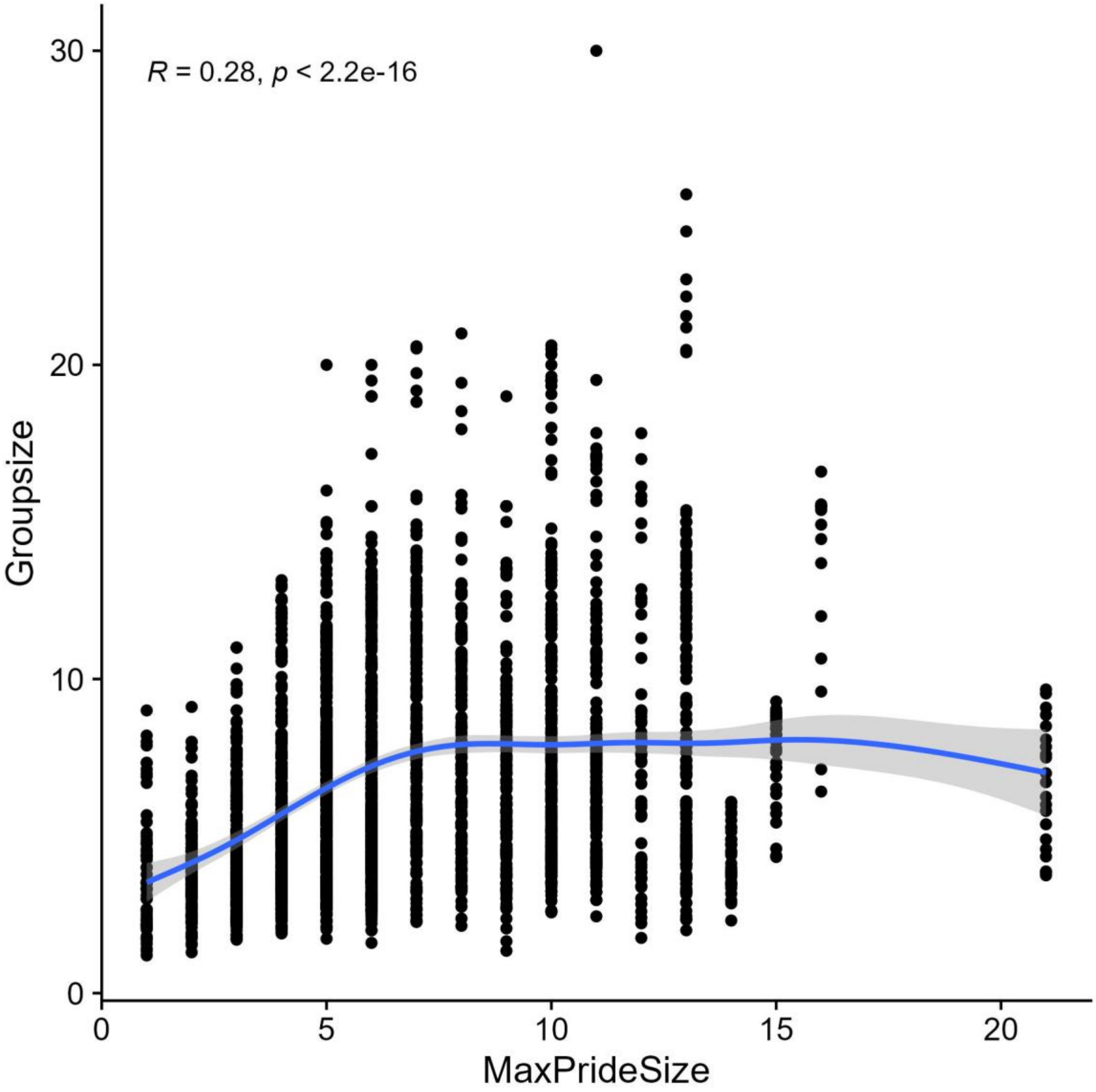


**Figure S3. Pearson's correlation plot for group size vs max pride size, Related to STAR Methods.** Points represent data for group size and max pride size, with the blue line and grey shaded area indicating the least squares regression line and 95% CI respectively. The correlation coefficient (R) and p value are shown on the plot (top left corner).

| Sex | Response | Explanatory | Estimate | Lower | Upper | P |
|---|---|---|---|---|---|---|
| F | Strength | Age | -0.044 | -0.065 | -0.023 | <0.001 |
| F | Strength | Age2 | -0.04 | -0.057 | -0.023 | <0.001 |
| F | Strength | Longevity | 0.042 | 0.018 | 0.065 | <0.001 |
| F | Strength.Female | Age | -0.072 | -0.097 | -0.048 | <0.001 |
| F | Strength.Female | Age2 | -0.009 | -0.029 | 0.01 | 0.354 |
| F | Strength.Female | Longevity | 0.039 | 0.012 | 0.066 | 0.004 |
| F | Strength.Male | Age | -0.004 | -0.033 | 0.026 | 0.801 |
| F | Strength.Male | Age2 | -0.067 | -0.091 | -0.043 | <0.001 |
| F | Strength.Male | Longevity | 0.035 | 0.003 | 0.068 | 0.030 |
| F | Degree | Age | 0.009 | -0.026 | 0.045 | 0.606 |
| F | Degree | Age2 | 0.005 | -0.023 | 0.034 | 0.724 |
| F | Degree | Longevity | 0.018 | -0.022 | 0.058 | 0.385 |
| F | Degree.Female | Age | 0.019 | -0.017 | 0.054 | 0.303 |
| F | Degree.Female | Age2 | 0.019 | -0.01 | 0.047 | 0.199 |
| F | Degree.Female | Longevity | 0.004 | -0.039 | 0.047 | 0.858 |
| F | Degree.Male | Age | -0.004 | -0.046 | 0.037 | 0.834 |
| F | Degree.Male | Age2 | -0.014 | -0.048 | 0.02 | 0.420 |
| F | Degree.Male | Longevity | 0.021 | -0.02 | 0.063 | 0.313 |
| F | Clustering | Age | 0.042 | -0.016 | 0.099 | 0.157 |
| F | Clustering | Age2 | -0.028 | -0.076 | 0.019 | 0.243 |
| F | Clustering | Longevity | -0.046 | -0.106 | 0.014 | 0.130 |
| F | Clustering.Female | Age | 0.027 | -0.035 | 0.089 | 0.393 |
| F | Clustering.Female | Age2 | -0.008 | -0.058 | 0.042 | 0.761 |
| F | Clustering.Female | Longevity | -0.063 | -0.126 | -0.001 | 0.047 |
| F | Mean_Strength | Age | -0.077 | -0.115 | -0.039 | <0.001 |
| F | Mean_Strength | Age2 | -0.056 | -0.087 | -0.025 | <0.001 |
| F | Mean_Strength | Longevity | 0.048 | 0.005 | 0.091 | 0.029 |
| F | Mean_Strength.Female | Age | -0.118 | -0.159 | -0.078 | <0.001 |
| F | Mean_Strength.Female | Age2 | -0.032 | -0.065 | 0 | 0.052 |
| F | Mean_Strength.Female | Longevity | 0.047 | -0.001 | 0.095 | 0.054 |
| F | Mean_Strength.Male | Age | 0.01 | -0.029 | 0.048 | 0.633 |
| F | Mean_Strength.Male | Age2 | -0.086 | -0.118 | -0.054 | <0.001 |
| F | Mean_Strength.Male | Longevity | 0.032 | -0.007 | 0.071 | 0.109 |
| F | Groupsize | Age | 0.081 | 0.034 | 0.127 | 0.001 |
| F | Groupsize | Age2 | -0.028 | -0.065 | 0.009 | 0.142 |
| F | Groupsize | Longevity | -0.013 | -0.062 | 0.036 | 0.604 |
| M | Strength | Age | -0.103 | -0.167 | -0.038 | 0.002 |
| M | Strength | Age2 | 0.007 | -0.038 | 0.052 | 0.763 |
| M | Strength | Longevity | 0.027 | -0.034 | 0.088 | 0.385 |
| M | Strength.Female | Age | 0.038 | -0.034 | 0.111 | 0.300 |
| M | Strength.Female | Age2 | -0.075 | -0.127 | -0.024 | 0.004 |
| M | Strength.Female | Longevity | 0.008 | -0.064 | 0.079 | 0.830 |
| M | Strength.Male | Age | -0.321 | -0.399 | -0.243 | <0.001 |
| M | Strength.Male | Age2 | 0.131 | 0.074 | 0.187 | <0.001 |
| M | Strength.Male | Longevity | 0.087 | -0.001 | 0.178 | 0.054 |
| M | Degree | Age | 0.137 | 0.054 | 0.221 | 0.001 |
| M | Degree | Age2 | -0.119 | -0.178 | -0.059 | <0.001 |
| M | Degree | Longevity | 0.148 | 0.069 | 0.227 | <0.001 |
| M | Degree.Female | Age | 0.172 | 0.087 | 0.258 | <0.001 |

| | | | | | | |
|---|---|---|---|---|---|---|
| M | Degree.Female | Age2 | -0.137 | -0.199 | -0.075 | <0.001 |
| M | Degree.Female | Longevity | 0.134 | 0.046 | 0.222 | 0.003 |
| M | Degree.Male | Age | 0.025 | -0.067 | 0.118 | 0.595 |
| M | Degree.Male | Age2 | -0.033 | -0.097 | 0.031 | 0.314 |
| M | Degree.Male | Longevity | 0.087 | 0.002 | 0.173 | 0.045 |
| M | Clustering | Age | 0.003 | -0.124 | 0.13 | 0.962 |
| M | Clustering | Age2 | 0.118 | 0.024 | 0.211 | 0.013 |
| M | Clustering | Longevity | -0.17 | -0.284 | -0.056 | 0.004 |
| M | Clustering.Male | Age | -0.049 | -0.186 | 0.089 | 0.486 |
| M | Clustering.Male | Age2 | 0.056 | -0.043 | 0.154 | 0.267 |
| M | Clustering.Male | Longevity | -0.055 | -0.184 | 0.073 | 0.396 |
| M | Mean_Strength | Age | -0.185 | -0.278 | -0.091 | <0.001 |
| M | Mean_Strength | Age2 | 0.111 | 0.042 | 0.18 | 0.002 |
| M | Mean_Strength | Longevity | -0.01 | -0.114 | 0.094 | 0.843 |
| M | Mean_Strength.Female | Age | -0.031 | -0.126 | 0.063 | 0.518 |
| M | Mean_Strength.Female | Age2 | 0.045 | -0.024 | 0.115 | 0.203 |
| M | Mean_Strength.Female | Longevity | -0.069 | -0.174 | 0.035 | 0.191 |
| M | Mean_Strength.Male | Age | -0.283 | -0.381 | -0.184 | <0.001 |
| M | Mean_Strength.Male | Age2 | 0.141 | 0.071 | 0.211 | <0.001 |
| M | Mean_Strength.Male | Longevity | 0.03 | -0.07 | 0.129 | 0.552 |
| M | Groupsize | Age | 0.172 | 0.064 | 0.279 | 0.002 |
| M | Groupsize | Age2 | -0.054 | -0.129 | 0.022 | 0.162 |
| M | Groupsize | Longevity | -0.046 | -0.147 | 0.055 | 0.367 |

**Table S1. Base model + SPDE effect estimates for both single sex models**, **Related to Figure 1, Figure 2, Figure 3 and STAR Methods.** Table shows the age, age$^2$, and longevity effects ("Explanatory" column) for each of the social metrics tested. "Focal Sex" indicates the model (F= female, M= male), "Response" indicates the response metric and target sex (e.g., Strength.Female = strength of associations to females from the focal sex).

# 3. The interplay between individual loss and social behaviour in the African lion

## 3.1. Abstract

Investigating the social predictors and consequences of individual loss for the sociality of the remaining population is an issue of great interest. Despite this, few studies have addressed such questions in a wild system. By applying spatial-social network analyses to 30 years of association data from over 500 wild African lions *(Panthera leo)*, we assessed (at the individual-level) social network metric changes prior to disappearance, alongside shifts in the social network metrics of remaining individuals following the loss of their associates. Strong sex-specific patterns emerged. Female social behaviour change was evident in both the year prior to, and year of, their disappearance from the system. They displayed overall reductions in the quality and quantity of their associations, but an increase in group size, in the year they were lost. In addition, in the year prior to disappearing they displayed reduced bond strength to other females. Conversely, we found no evidence of male social network metric shifts prior to their disappearance. However, male lions did respond socially to the loss of their male associates- their bond strength to females increased, but their number of female associates and average group size decreased. Female lions also responded

to the loss of their male associates with reduced average group size, while the loss of female associates led to a decrease in their connectivity strength and bond strength. The inclusion of ageing and longevity effects in the models further suggest that pre-disappearance social shifts and associate loss may explain social ageing in females, but not in males. Understanding such fluctuations in the social dynamics of wild lion populations will be important in aiding conservation of the species, due to the interplay between sociality and phenomena such as disease transmission and information transfer via social learning. Future studies should consider the drivers of individual disappearance, and the potential for other demographic characteristics such as age, to influence individual-variation in response to associate loss.

## 3.2. Introduction

Understanding how natural populations respond to the loss or turnover of individuals is currently of much interest to ecology and conservation biology. Wild animal social systems are shaped by demographic processes (such as death, dispersal, and reproduction rates), and individual-level social behaviour[1]. The interaction between demography and behaviour ultimately shapes the opportunities for, and nature of, social associations between individuals. For example, changes in group size or group composition have been shown to relate to inter-individual affiliative interactions[2,3], aggressive interactions[4], and overall cohesion[5]. Within-individual changes in social behaviour over time (e.g. due to ageing) also have knock-on effects on the sociality of their associates, and the wider population[6–9]. These effects can interact with the demographic characteristics of both the individual and their groupmates, which may in turn influence social behaviour in relation to key processes such as mating and reproduction. As such, demographically and behaviourally driven temporal changes in sociality can alter fitness, and the social structure and stability of a population.

Recent methodological developments have facilitated structured investigation of the causes and consequences of fine-scale sociality across animal societies, through considering these within the framework of 'social networks'[10,11]. Such network methods allow temporal changes in social association patterns to be tracked and quantified in a consistent way within and across populations. This allows social dynamics to be understood at the level of individual differences in behaviour, while simultaneously allowing population-wide effects to be considered. Such methods have been applied to understanding the dynamics of phenomena including disease transmission[12,13], information spread[14–16], and the lifetime impacts of early-life experience[17–19]. Yet, the primary and most obvious change to social systems occurs through the loss of individuals.

Most investigations of social disturbance from loss have been carried out either in birds[5,20–22] or small mammals[23,24]. Others have focused on hierarchically structured systems, and the impact of "catastrophic" events that sharply increase mortality. For example, African elephant (*Loxodonta africana*) social systems are resilient to the loss of older individuals due to poaching, through the transmission of social roles from mothers to daughters[25]. Conversely, at a population level killer whale (*Orcinus orca*) networks are vulnerable to the simulated removal of individuals that mimic historic live-capture mortality (based on sex and age)[26]. Individual killer whales were further found to alter the quantity and quality of their social associations following an additive mortality event[27]. Similarly, extreme weather induced mortality in an isolated population of Rhesus macaques (*Macaca mulatta*) resulted in an increase in affiliative social partners amongst remaining individuals, especially those that were previously socially isolated[28]. While such studies have been illuminating, we lack understanding of behavioural and social responses to ongoing individual turnover in populations over long timescales.

It is becoming increasingly recognised that the loss of individuals may have carry over effects onto remaining individuals through reducing social connectivity. Indeed, being socially well-connected impacts longevity and fitness across species[29–34]. Two general hypotheses regarding the mechanisms behind this have been proposed. The "social buffering" hypothesis suggests that associates offer protection against stressors such as disease[35], while the "main effects" hypothesis suggests social relationships directly provide aid (whether emotional or behavioural) that encourage healthy behaviours[36]. Such effects are likely to be of most importance to group living species, where solitaires are vulnerable and so the costs of isolation are inherently more profound[37]. By extension, the loss of group members may confer a cost on their prior associates. The extent of such costs could be influenced by the characteristics (e.g. sex) and social position of the individual lost, and the demography of the remaining population. In addition, the prior nature of the relationship between individuals is likely to shape the impact of one's disappearance on the other, and the broader social system (whether that disappearance be due to death or dispersal)[21].

While the loss of individuals may affect the size and composition of social groups, changes in within-individual social behaviour can also interact with group-level changes. Specifically, ‘social ageing’ (i.e. the change of individual social behaviour with age), research across primates and ungulates has produced evidence of changes in the sociality of individuals towards the end of their lifespan[38,39]. There have further been indications of differing patterns of social ageing between sexes in species with divergent sex roles[40]. However, less explored are changes in the social behaviour of individuals prior to their disappearance. While senescence is one likely predictor of individual mortality[41,42], there are a suite of additional drivers of individual loss from populations including dispersal, eviction, and pre-senescent mortality due to disease or competition. Given the interplay between sociality and many such processes[43–48], it is plausible that social indicators of imminent disappearance (such as declining social integration) would exist for individuals of all ages.

The African lion (*Panthera leo*) represents a unique opportunity to investigate the dynamics surrounding social disturbances in a group-living apex predator. Despite knowledge that factors such as ageing[40] and prey availability[49] impact sociality, little is known about the consequences of naturally occurring social perturbations to this egalitarian, fission-fusion system[50]. Using social network analyses conducted on 30 years of data from 590 lions in the wild Serengeti population (354 females, 236 males; 60121 total observations), we investigate the relationship between individual level social behaviour and loss of associates. Specifically, we consider how individuals’ i) average group size, ii) number of associates (degree), iii) total sum of weighted social associations to others (strength), and iv) social bond strength to associates (mean strength) relate to loss. We further investigate the response of individuals to the loss of their associates by examining whether the prior strength of associations to lost individuals predicts changes in their own social behaviour (measured as the above metrics i to iv) in the subsequent year. Additionally, we consider how the sex of lost individuals differentially impacts the sociality of their remaining associates. In this way, we analyse the relationship between loss and social behaviour in a wild population, and conclude by discussing the significance of these findings across animal systems.

## 3.3. Methods

### 3.3.1. Study system and data collection

The research data were collected on a long-studied population of African lions inhabiting a 2700km2 study area within the Serengeti National Park, Tanzania. This habitat includes both a grassland plains and woodland area. There are two broad seasons, the wet season spanning November to May, and the dry season spanning June to October. The woodlands habitat remains relatively stable year-round, while the grasslands habitat experiences higher fluctuations in rainfall, resulting in seasonal migrations of prey species (with lower densities in the dry season). Lion pride territories routinely shift geographically across the seasons with prey species migrations[51].

Female lions live in fission-fusion prides throughout the study area, composed of related adults and their offspring. Prides range in size from 2-20 individuals, but individuals are most often found in smaller sub-groups (and commonly spend time alone). These subgroups vary in composition and size from day to day, but female pride-mates usually stay within 5-6 km of each other. Approximately 75% of female offspring are recruited back into the mother's pride, while 25% disperse to form new prides (often in adjacent territories) after the age of two years[50,52].

Conversely, all male offspring disperse from the natal pride in cohorts of kin (usually brothers and cousins) between the ages of two - four. Kin cohorts may form alliances during this "nomadic" life stage, resulting in coalitions of up to nine males. Most coalitions "take over" residence of their own pride by the age of four, which is when males reach full body size[50,52]. Once this happens, coalition membership does not change (except for loss of individuals to mortality). Reproductive success is highest in males aged 4-14 years old[53]. There is no clear dominance hierarchy between female pride mates or male coalition mates [50,54].

The data used in this study were collected over 30 years between 1984 and 2013, during which time 1 female per pride was fitted with a GPS collar. Each collared individual was located at least once every two weeks, and individuals within 200m of each other were considered to be co-occurring. These individuals were recorded as part of the same sighting event using a GPS location, date and time stamp. Opportunistic sightings of individuals within the study area were also recorded. Facial markings and whisker spots were used to identify individuals to a high degree of accuracy. For each individual, age (estimated from the date of first sighting as a cub or adult), sex, natal pride (if born in the study site), and current pride data was also available. Only data on individuals observed in the two consecutive years prior to death/disappearance were included. For this reason, and following prior work in this system[40], individuals were only included from age 3 onwards, yielding 354 females and 236 males.

### 3.3.2. Social networks and individual metrics

We compared social networks based on seasonal and annual data aggregations and observed that both network-level and individual-level metrics remained similar across temporal scales. As such, to maximise the number of observations per individual in each network, and following previous work in this system[40], social networks were created at yearly intervals following the seasonal calendar (start of dry season to end of wet season), for 30 years from June 1984 onwards. The network “nodes” constituted individual lions and the “edges” constituted dyadic associations between them. Using the “gambit of the group” method[55], individuals were considered to be associating if they were observed in the same sighting event (as described above) according to the recorded date and GPS location. As in[40] and many other animal social network studies[56], the Simple Ratio Index (SRI) was then applied to the yearly grouping event and used to calculate dyadic associations[57], giving the proportion of overall sightings in which two individuals were observed together rather than the absolute count. All SRI values range between 0 (individuals never seen together) and 1 (individuals always seen together).

### 3.3.3. Predictors of loss

To investigate social predictors of individual disappearance from the population, we used the annual networks to derive four metrics that are known to vary with age and impact longevity in African lions[40]. We examined these metrics in both the year the individual was last seen (referred to hereafter as the “final year”), and the year prior to that (referred to hereafter as the “penultimate year”). We tested the following predictors:

a) Group size: the average number of other individuals the focal lion was observed with per sighting

b) Degree: the number of unique individuals the focal lion was observed with over the course of the year

c) Strength: the total weighted sum of the focal lion’s associations within the network over the course of the year (quantifying overall connectivity)

d) Mean strength: the total sum of the focal lion’s weighted associations to its associates over the course of the year (quantifying bond strength)

### 3.3.4. Response to loss

To assess the impact of losing associates on individual-level social behaviour, for every yearly network we identified individuals that were lost in the following year (lost individuals) and those that survived the following year (focal individuals). We then calculated each focal individual's strength (weighted sum of their associations) to only the identified lost individuals that year. We assigned this “strength to lost individuals” metric to the focal individual as a trait in the following year. As such this trait was a proxy for the social impact[21] of associate loss experienced by the focal individual. We assessed the effect of this explanatory "social impact" factor, in combination with the sex (male or female) of the lost associates, on the social metrics derived as described above. The metrics were each fitted as a response variable in a separate set of models.

### 3.3.5. Ageing and longevity effects

Longevity and age effects were included in the models as in[40], so that any compounding effects of these factors on predictors of loss and response to loss could be identified.

### 3.3.6. Modelling details

Across all models, we fitted linear models using the Integrated Nested Laplace Approximation (INLA) and analysed female associations and male associations separately (both to females only and males only). Only data on individuals age > 3 were analysed. Each model included the following fixed explanatory variables: final year (binary variable, representing whether the individual died in the current year); penultimate year (binary variable, representing whether the individual died in the following year); strength to lost female (continuous, social impact of female associate loss), strength to lost male (continuous, social impact of male associate loss), age (continuous, in years); longevity (continuous, age at disappearance in years); number of observations (continuous, the number of times an individual was seen that year); group size (continuous, an annual mean from the observation data); foreign (binary variable, representing whether or not the individual was born in the study area); and collared (binary variable, representing whether or not they had a GPS collar). We also included three random effects: natal pride (the pride in which an individual was born); pride (the pride in which an individual was most often seen in a given year); year; and individual identity.

Using INLA models we were also able to fit a stochastic partial differentiation equation (SPDE) effect to account for spatiotemporal autocorrelation as in previous social network analyses using this study system[40]. To investigate spatial dependence, we used each individual's average X and Y coordinate in each year (i.e., their annual spatial centroid); the effect modelled the expectation that individuals will have more similar social network positions when their locations were closer in space. To assess whether the models were significantly spatially autocorrelated, we first fitted the base model, and then added the SPDE effect and compared the model fit using deviance information criterion (DIC). We took 5 DIC to differentiate between competitive models, such that if the SPDE effect reduced DIC by more than 5 it was taken to be significantly autocorrelated (Figure S1). $R^2$ values for the final models and social network metric correlation plots can be found in Figures S2 and S3 respectively.

## 3.4. Results

Over the 30-year study period, 60121 sightings of 354 female and 236 male lions were used to generate annual social networks (mean sightings per individual; SE = 23.11; 0.36). A total of 92 females were lost from the population, at a mean age of 10.86 +/- 0.39 (mean +/- SE). A total of 81 males were lost from the population at a mean age of 7.24 +/- 0.30 (mean +/- SE). This equated to 5.97 +/- 0.713 individuals lost per year (mean +/- SE).

### 3.4.1. Predictors of loss

We found significant changes in the sociality of females in both their penultimate and final year present in the population (Figure 1, Table S1). This was evident through reductions in their number of associates and the decreased connectivity of individuals that were subsequently lost from the population. All such effects were present even when controlling for the number of observations per individual each year, which would most likely be lower in the year that they were lost from the system (the final year). Conversely, there were no significant changes in sociality of males before they disappeared.

Female group size was significantly higher in the final year (estimate= 0.294; CI= 0.099, 0.489; p= 0.003). Conversely, there was a significant effect of lower intra-sex degree (estimate= -0.147; CI= -0.294, -0.001; p= 0.049), and inter-sex degree (estimate= -0.194; CI= -0.376, -0.012; p= 0.036) in the final year they were present in the population. In addition, females had significantly lower intra-sex strength in both the final and penultimate year (final- estimate= -0.382; CI= -0.484, -0.279; p<0.001; penultimate- estimate= -0.118; CI= -0.178, -0.059; p<0.001). Female inter-sex strength in the final year was similarly lower (estimate= -0.334; CI= -0.465, -0.202; p<0.001). Females also had significantly lower intra-sex mean strength (estimate= -

0.402; CI= -0.571, -0.234; p<0.001), and inter-sex mean strength (estimate= -0.332; CI= -0.503, -0.162; p<0.001) in their final year in the population (Figure 1).

### 3.4.2. Response to loss

The effect of associate loss on sociality varied between the sexes, and depended on the sex of the associates they lost (Figure 1, Table S2). For both females and males, the effects of same-sex associate loss were more profound. However, female group size did significantly decrease with strength to lost males in the previous year (estimate= -0.097; CI= -0.176, -0.019; p= 0.015; Figure 2), as did male group size (estimate= -0.184; CI= -0.359, -0.008; p= 0.040; Figure 3). There was no effect of associate loss on female degree. However, male intra-sex degree decreased with strength to lost male adults (estimate= -0.314; CI= -0.460, -0.168; p<0.001; Figure 3).

With increasing strength to lost females, female intra-sex strength significantly decreased (estimate= -0.062; CI= -0.105, -0.019; p= 0.004; Figure 2). Bond strength followed similar patterns, with a significant decline in female intra-sex mean strength with strength to lost females (estimate= -0.114; CI= -0.185, -0.043; p= 0.002; Figure 2). Conversely, male inter-sex mean strength increased with strength to lost female associates (estimate= 0.172; CI= 0.015, 0.328; p= 0.032; Figure 3).

### 3.4.3. Ageing and longevity effects

In combination with the effects of individual sociality change prior to disappearance and associate loss, we continued to detect social ageing and longevity effects in both sexes (Table S3). However, in females the only significant effect was a decline in intra-sex mean strength with age (estimate= -0.056; CI= -0.104, -0.008; p= 0.023; Figure 1). No significant longevity effects were found.

Male group size significantly increased with age (estimate= 0.145; CI= 0.019, 0.270; p= 0.024), as did male inter-sex degree (estimate= 0.180; CI= 0.071, 0.289; p= 0.001). Further, male intra-sex strength decreased with age (estimate= -0.244; CI= -0.338, -0.150; p< 0.001), as did male intra-sex mean strength (estimate= -0.171; CI= -0.282, -0.060; p= 0.003). Males also exhibited a significant effect of intra-sex degree on longevity (estimate= 0.119; CI= 0.0003, 0.237; p= 0.049; Figure 1).

## 3.5. Discussion

By applying social network analysis to 30 years of data detailing associations amongst wild lions, we show the interplay between individual loss and social behaviour. Specifically, we show that individual lionesses' sociality changes in the year prior to, and year of, their loss from the population. Additionally, we show that individual-level sociality is differentially vulnerable to the loss of associates dependent on the remaining individual's sex, as well as the sex of the lost individual. These findings were evident even when accounting for age and longevity effects in our models, suggesting the previously identified senescent declines in sociality[40] may partially be attributed to pre-disappearance changes in sociality and the loss of associates. Studies addressing similar questions to date have often considered only response to or predictors of disappearance, and relied on computer simulations or artificial experiments to induce individual loss[21,26]. By incorporating multiple components of disappearance from a wild population across a long timeframe, we gained a broader view of the dynamics surrounding social disturbances.

Understanding social predictors of disappearance is important in bolstering our knowledge of the social dynamics surrounding phenomena such as dispersal, eviction, and mortality.  Lionesses were less gregarious, less strongly connected, and less strongly bonded to their associates in their final year in the Serengeti population. This decline in the quantity and quality of female associations, despite being observed in larger group sizes, can be characterised as an overall “shrinking” of the network, as previously identified in ageing females[40]. Such patterns were only partially present in lionesses' penultimate year in the population, when there were evident declines in the strength of their intra-sex connections.

This could be indicative of reproductive senescence[58] in older individuals. However, not all individuals that disappeared from the population were aged. Mortality rates also remain relatively high throughout adulthood, owing to risks of injury during hunting, territorial fights and defence against intruding males[59]. Females older than 3 (the age of inclusion in the study) often disperse as prides splinter when infanticidal males take over pride residency, especially if they have cubs which otherwise would have been killed[60]. Similar dynamics exist in other social mammals, with the propensity of female yellow-bellied marmots to disperse being linked to the extent of their embeddedness within their social group[61]. In female rhesus macaques, similar reductions in social integration prior to eviction from the population have been observed[44]. However, this only applied to sociality between those who were evicted and those who remained, while social interactions and cliquishness amongst those that departed actually increased. Similar dynamics may be present amongst female lions that leave their pride as a cohort, so future studies should incorporate measures of the drivers of disappearance (e.g. dispersal due to infanticidal males) to elucidate this further.

Highlighting the importance of considering sex-based differences in social processes between the sexes, we found that in contrast to females, male lions did not exhibit changes in the quality or quantity of their associations prior to disappearing. This sits in contrast to existing knowledge (replicated in this study) that ageing male lions gain female associates and become less connected and closely bonded to other males[40]. To understand these results fully there is a need to consider the drivers of male disappearance. There is undoubtedly a role of physical fitness and the size of the coalition in retaining pride residency [50,53] which would suggest a role of senescence in predicting male disappearance. However, pride takeovers are relatively spontaneous events, and most males lost during adulthood will have been “ousted” or killed by competitors. Such events could occur at any time in a male's lifespan, as their vulnerability may be driven by other factors such as injury or disease[50], or simply the superior strength of their competitors. As such, detecting social predictors of male disappearance may be challenging, particularly with lower observation frequencies for males than females in this population. There is a need for targeted data collection on male sociality to improve our understanding of these dynamics.

Although the large-scale drivers of population declines and consequences of shrinking populations have been well documented, less is known about the social consequences of associate loss for surviving individuals. We found minimal evidence of strongly directional social behaviour change in lions following the loss of their associates from the population. Overall individuals were most impacted by the loss of same-sex associates. However, lion sociality remained relatively stable, particularly with regard to the number of associates, suggesting individuals mediate the effects of changes to associate availability within their existing networks.

Lions do not appear to compensate for losing associates by increasing the quantity of individuals they interact with. Both females and males were found in smaller sub-groups after the loss of adult males. Males additionally lost female associates but were more closely bonded to their remaining female associates. This raises important considerations in phenomena such as disease outbreaks, when periods of high-mortality may accentuate such shifts in the social landscape. Male Serengeti lions may be more at risk of exposure to pathogens than females due to their socio-spatial behaviour, and propensity to be resident in multiple prides[50]. This could increase their likelihood of contact with sick (intra and inter-specific) individuals[62]. Disease transmission might therefore be impacted by altered contact networks[13,63], with males more closely associating with females following the death of coalition mates, and therefore increasing exposure risk for females and cubs. Further, and as has been observed in other species [22,64,65], culling lions to control disease spread may have unintended consequences through perturbation induced changes to sociality. Such considerations are important in the Serengeti lion population which has been subject to severe outbreaks of canine distemper, with disease lethality exaggerated by climate extremes [66,67] suggesting it will continue to pose a threat under global climate change.

Lionesses did not replace the strength of their prior (and lost) intra-sex connections, with significant declines in both connectivity and the closeness of their bonds. We can hypothesise that this would impact fitness given lionesses' high dependence on pridemate cooperation for hunting, cub rearing and territoriality[50,68–70]. There could be additional consequences for social information transfer, especially if changes to social structuring have additional implications for spatial behaviour as in other social mammals[71,72]. Further investigation of such processes following disturbance to the social landscape are now needed. It will be particularly key to understand whether females rebuild stronger relationships over extended time periods beyond one year post associate loss. We continued to detect a negative effect of age on mean strength, suggesting it is unlikely that associate loss or pre-disappearance sociality changes fully explain declines in lioness bondedness. However, declines in the quality of relationships following the loss of close associates could be a strong contributor, particularly if it takes a long time for females to replace such associations. It is possible that ageing females are never fully able to do so before they die. This could have cascading effects on pride cohesion if the age structuring of the group makes this a vulnerability (e.g., if there are lots of old individuals).

Conversely to females, we found that males were vulnerable to the loss of their male associates, experiencing subsequent decreases in their number of female associates but increasing bond strength to them. This contrasts with the persistence of previously identified age and longevity effects[40], showing increases in group size and the number of female associates with age, plus a positive effect of the number of male associates on longevity. It is likely this reflects that larger coalitions are more successful in defending residency of prides[50], and by extension, the loss of coalition mates increases the probability of being outcompeted by intruding coalitions. Males that are able to retain their coalition mates live longer and perhaps this facilitates the continual growth of their pride. Similarly, the disappearance of coalition mates could increase the likelihood of pride fission or female dispersal[45], thereby altering the availability of females for the remaining males.

Lion sociality is such that the individual turnover is not unusual. Not only does the fission-fusion system itself permit fluctuation in associate presence, but so do natural demographic phenomena such as the splintering of large prides and dispersal of sub-adults[45,46,52]. Additionally, infanticide by intruding males can force the emigration of mothers with cubs or sub-adults[60]. Such events all lead to alterations in the availability of con specifics for remaining individuals to interact with. Our findings suggest several mechanisms by which individuals maintain social resilience to this change, which are largely dependent on the sex of the individuals involved. This is unsurprising given the sex-based differences in reproductive and social behaviour, and so differences in dependence on conspecifics throughout the life cycle[40,45,50,52,60].

Losing associates, especially those with previously close relationships, has been shown to alter subsequent social interaction networks across species[21,27,72–75]. As such understanding social predictors of loss, and the impacts of loss on remaining individuals, is of great ecological and evolutionary interest. For a charismatic and threatened species such as the African lion, it is also of huge importance for conservation efforts. Perturbations due to climate change, disease, habitat loss and conflict with humans will all have consequences for population social dynamics. Of particular interest may be the varied impacts that loss of specific demographics causes. Against a backdrop of ongoing contention surrounding the ethics and impacts of trophy hunting[76–80], we found minimal evidence that the loss of adult males shifted female social dynamics, but it did impact the sociality of remaining males. The disappearance of adult females did not impact males but caused declines in the quality of intra-sex female relationships. Threats most pertinent to lionesses (e.g. human-wildlife conflict[81]) should therefore also be considered in the context of potential effects of social perturbations, particularly on cooperative behaviours that are key to survival, such as hunting, territoriality, and cub rearing[68–70,82,83].

## 3.6. Conclusions

Our results offer novel insights into the impacts of disturbance via individual loss to social networks, both from the perspective of the focal individual and the individuals remaining in the population. We show that changes in the availability of associates, and the behavioural response of others to this, creates persistent flux in the social system. Additionally, we provide evidence to suggest that drivers of social ageing in African lions likely vary substantially between the sexes. While within-individual changes and associate loss appear important contributors in females, they are not for males.

It will be key for future studies to consider the potential drivers of disappearance and additional individual demographic characteristics (both of lost and remaining individuals) such as age. Further investigating the specific characteristics of spatial behaviour changes alongside social behaviour changes would facilitate improved predictions of the effects of social disturbance on disease spread and information transfer, which may be important for conservation management. In all cases, examining such phenomena is largely dependent on the availability of data from long-term studies, particularly in species with long generation times. The availability of such data on species with diverse social systems will be essential to expanding knowledge of the fitness consequences of social disturbances to wild populations.

## 3.7. Figures

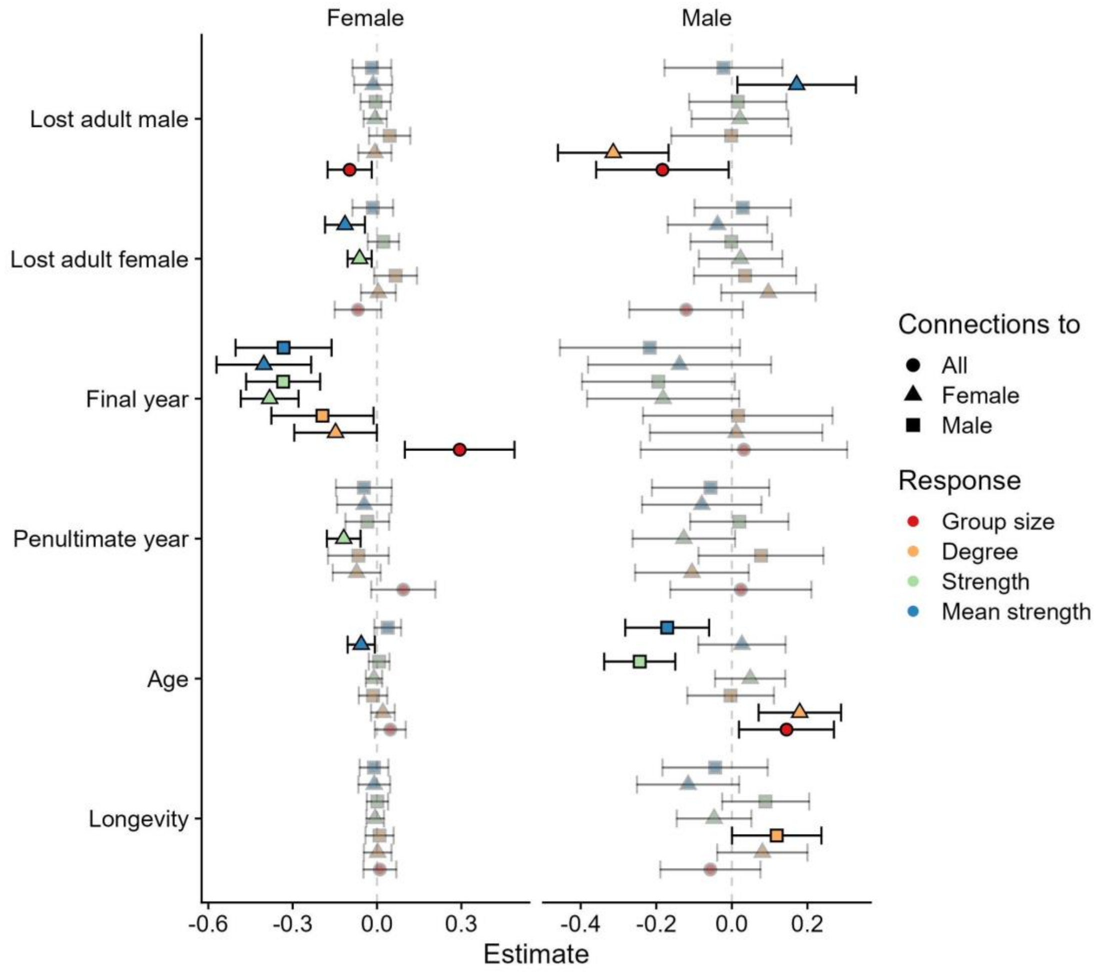


**Figure 1. Associations between responses to loss, predictors of loss, age, longevity and social metrics.** Estimates taken from SPDE single sex model for females (left) and males (right), showing the loss of male associates, loss of female associations, final year, penultimate year, age and longevity effects for each social metric tested. Points represent the model estimate with error bars showing the 95% Credibility Intervals (estimated according to the 95% upper and lower quantiles of the posterior density distribution for each effect). Bold points indicate a significant relationship, faded points indicate a non-significant relationship.

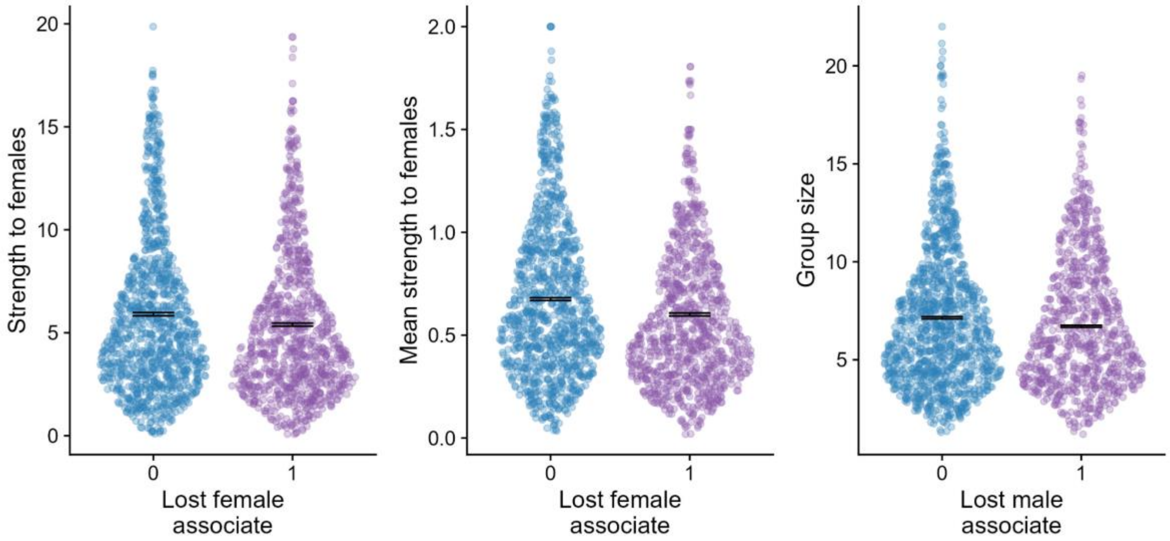


**Figure 2. Social response of females to the loss of their associates.** Plots from left to right show females strength to females following the loss of 0 (x axis = 0) or 1+ (x axis = 1) female associate; females mean strength to females following the loss of 0 (x axis = 0) or 1+ (x axis = 1) female associate; female group size following the loss of 0 (x axis = 0) or 1+ (x axis = 1) male associate. Points show the raw data with bars representing the SPDE model predicted means +/- the standard error.

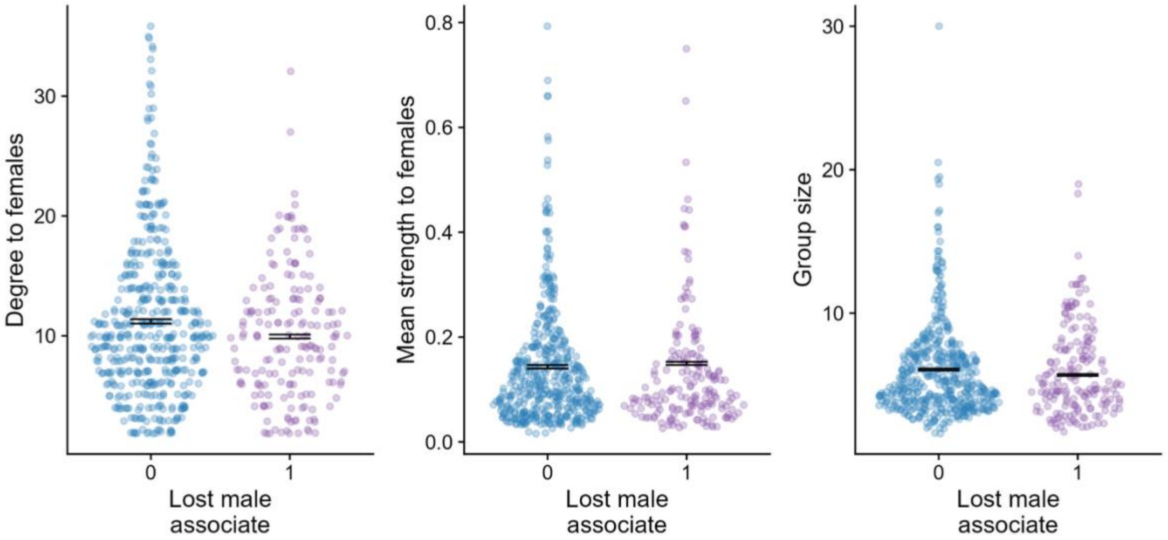


**Figure 3. Social response of males to the loss of their associates.** Plots from left to right show male degree to females following the loss of 0 (x axis = 0) or 1+ (x axis = 1) male associate; male mean strength to females following the loss of 0 (x axis = 0) or 1+ (x axis = 1) male associate; male group size following the loss of 0 (x axis = 0) or 1+ (x axis = 1) male associate. Points show the raw data with bars representing the SPDE model predicted means +/- the standard error.

## 3.8. References

1. Shizuka, D., and Johnson, A.E. (2020). How demographic processes shape animal social networks. Behav. Ecol. *31*, 1–11. https://doi.org/10.1093/beheco/arz083.

2. Kurihara, Y., Nishikawa, M., and Mochida, K. (2019). Behavioral responses to changes in group size and composition: a case study on grooming behavior of female Japanese macaques (Macaca fuscata yakui). Behav. Processes *162*, 142–146. https://doi.org/10.1016/j.beproc.2019.03.005.

3. Mirville, M.O., Ridley, A.R., Samedi, J.P.M., Vecellio, V., Ndagijimana, F., Stoinski, T.S., and Grueter, C.C. (2020). Intragroup Behavioral Changes Following Intergroup Conflict in Mountain Gorillas (Gorilla beringei beringei). Int. J. Primatol. *41*, 382–400. https://doi.org/10.1007/s10764-020-00130-1.

4. Asensio, N., Aureli, F., Schaffner, C., and Korstjens, A. (2008). Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. Behaviour *145*, 983–1001. https://doi.org/10.1163/156853908784089234.

5. Genovart, M., Gimenez, O., Bertolero, A., Choquet, R., Oro, D., and Pradel, R. (2020). Decrease in social cohesion in a colonial seabird under a perturbation regime. Sci. Rep. *10*, 18720. https://doi.org/10.1038/s41598-020-75259-3.

6. Woodman, J., Gokcekus, S., Beck, K., Green, J., Nussey, D., and Firth, J. (2024). The ecology of ageing in wild societies: linking age structure and social behaviour in natural populations (Life Sciences) https://doi.org/10.32942/X21893.

7. Albery, G.F., Clutton-brock, T.H., Morris, A., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2021). Ageing red deer alter their spatial behaviour and become less social Abstract Introduction Results.

8. Siracusa, E.R., Pereira, A.S., Brask, J.B., Valle, J.E.N.-D., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. Ageing in a collective: the impact of ageing individuals on social network structure.

9. Siracusa, E.R., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Within-individual changes reveal increasing social selectivity with age in rhesus macaques. Proc. Natl. Acad. Sci. *119*, e2209180119. https://doi.org/10.1073/pnas.2209180119.

10. Krause, J., Croft, D.P., and James, R. (2007). Social network theory in the behavioural sciences: potential applications. Behav. Ecol. Sociobiol. *62*, 15–27. https://doi.org/10.1007/s00265-007-0445-8.

11. Sih, A., Hanser, S.F., and McHugh, K.A. (2009). Social network theory: new insights and issues for behavioral ecologists. Behav. Ecol. Sociobiol. *63*, 975–988. https://doi.org/10.1007/s00265-009-0725-6.

12. Albery, G.F., Kirkpatrick, L., Firth, J.A., and Bansal, S. (2021). Unifying spatial and social network analysis in disease ecology. J. Anim. Ecol. *90*, 45–61. https://doi.org/10.1111/1365-2656.13356.

13. Silk, M.J., Croft, D.P., Delahay, R.J., Hodgson, D.J., Boots, M., Weber, N., and McDonald, R.A. (2017). Using social network measures in wildlife disease ecology, epidemiology, and management. BioScience *67*, 245–257. https://doi.org/10.1093/biosci/biw175.

14. Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. Proc. R. Soc. B Biol. Sci. *279*, 4199–4205. https://doi.org/10.1098/rspb.2012.1591.

15. Boogert, N.J., Nightingale, G.F., Hoppitt, W., and Laland, K.N. (2014). Perching but not foraging networks predict the spread of novel foraging skills in starlings. Behav. Processes *109*, 135–144. https://doi.org/10.1016/j.beproc.2014.08.016.

16. Chiyo, P.I., Moss, C.J., and Alberts, S.C. (2012). The influence of life history milestones and association networks on crop-raiding behavior in male african elephants. PLoS ONE *7*. https://doi.org/10.1371/journal.pone.0031382.

17. McDonald, D.B. (2007). Predicting fate from early connectivity in a social network. Proc. Natl. Acad. Sci. U. S. A. *104*, 10910–10914. https://doi.org/10.1073/pnas.0701159104.

18. Stanton, M.A., and Mann, J. (2012). Early Social Networks Predict Survival in Wild Bottlenose Dolphins. PLoS ONE *7*, 1–6. https://doi.org/10.1371/journal.pone.0047508.

19. Turner, J.W., Robitaille, A.L., Bills, P.S., and Holekamp, K.E. (2021). Early-life relationships matter: Social position during early life predicts fitness among female spotted hyenas. J. Anim. Ecol. *90*, 183–196. https://doi.org/10.1111/1365-2656.13282.

20. Lantz, S.M., and Karubian, J. (2017). Environmental disturbance increases social connectivity in a passerine bird. PLoS ONE *12*, 1–15. https://doi.org/10.1371/journal.pone.0183144.

21. Firth, J.A., Voelkl, B., Crates, R.A., Aplin, L.M., Biro, D., Croft, D.P., and Sheldon, B.C. (2017). Wild birds respond to flockmate loss by increasing their social network associations to others. Proc. R. Soc. B Biol. Sci. *284*. https://doi.org/10.1098/rspb.2017.0299.

22. Downing, B.C., Silk, M.J., Delahay, R.J., Bearhop, S., and Royle, N.J. (2023). Culling-induced perturbation of social networks of wild geese reinforces rather than disrupts associations among survivors. J. Appl. Ecol. *60*, 2613–2624. https://doi.org/10.1111/1365-2664.14522.

23. Evans, J.C., Liechti, J.I., Boatman, B., and König, B. (2020). A natural catastrophic turnover event: Individual sociality matters despite community resilience in wild

house mice. Proc. R. Soc. B Biol. Sci. *287*, 1–9. https://doi.org/10.1098/rspb.2019.2880.

24. Gall, G.E.C., Evans, J.C., Silk, M.J., Ortiz-Jimenez, C.A., and Smith, J.E. (2022). Short-term social dynamics following anthropogenic and natural disturbances in a free-living mammal. Behav. Ecol. *33*, 705–720. https://doi.org/10.1093/beheco/arac032.

25. Goldenberg, S.Z., Douglas-Hamilton, I., and Wittemyer, G. (2016). Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks. Curr. Biol. *26*, 75–79. https://doi.org/10.1016/j.cub.2015.11.005.

26. Williams, R., and Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. Biol. Lett. *2*, 497–500. https://doi.org/10.1098/rsbl.2006.0510.

27. Busson, M., Authier, M., Barbraud, C., Tixier, P., Reisinger, R.R., Janc, A., and Guinet, C. (2019). Role of sociality in the response of killer whales to an additive mortality event. Proc. Natl. Acad. Sci. U. S. A. *116*, 11812–11817. https://doi.org/10.1073/pnas.1817174116.

28. Testard, C., Larson, S.M., Watowich, M.M., Kaplinsky, C.H., Bernau, A., Faulder, M., Marshall, H.H., Lehmann, J., Ruiz-Lambides, A., Higham, J.P., et al. (2021). Rhesus macaques build new social connections after a natural disaster. Curr. Biol. *31*, 2299-2309.e7. https://doi.org/10.1016/j.cub.2021.03.029.

29. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. Curr. Biol. *20*, 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067.

30. Ellis, S., Snyder-Mackler, N., Ruiz-Lambides, A., Platt, M.L., and Brent, L.J.N. (2019). Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. Proc. R. Soc. B Biol. Sci. *286*, 20191991. https://doi.org/10.1098/rspb.2019.1991.

31. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., and Cheney, D.L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc. R. Soc. B Biol. Sci. *276*, 3099–3104. https://doi.org/10.1098/rspb.2009.0681.

32. Frère, C.H., Krützen, M., Mann, J., Connor, R.C., Bejder, L., and Sherwin, W.B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. Proc. Natl. Acad. Sci. *107*, 19949–19954. https://doi.org/10.1073/pnas.1007997107.

33. Cameron, E.Z., Setsaas, T.H., and Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. Proc. Natl. Acad. Sci. U. S. A. *106*, 13850–13853. https://doi.org/10.1073/pnas.0900639106.

34. Archie, E.A., Tung, J., Clark, M., Altmann, J., and Alberts, S.C. (2014). Social

affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. Proc. R. Soc. B Biol. Sci. *281*. https://doi.org/10.1098/rspb.2014.1261.

35. Kikusui, T., Winslow, J.T., and Mori, Y. (2006). Social buffering: relief from stress and anxiety. Philos. Trans. R. Soc. B Biol. Sci. *361*, 2215–2228. https://doi.org/10.1098/rstb.2006.1941.

36. Holt-Lunstad, J., Smith, T.B., and Layton, J.B. (2010). Social Relationships and Mortality Risk: A Meta-analytic Review. PLoS Med. *7*. https://doi.org/doi:10.1371/journal.pmed.1000316.

37. Lucas, E.R., and Keller, L. (2020). The co-evolution of longevity and social life. Funct. Ecol. *34*, 76–87. https://doi.org/10.1111/1365-2435.13445.

38. Machanda, Z.P., and Rosati, A.G. (2020). Shifting sociality during primate ageing. Philos. Trans. R. Soc. B Biol. Sci. *375*, 20190620. https://doi.org/10.1098/rstb.2019.0620.

39. Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2022). Ageing red deer alter their spatial behaviour and become less social. Nat. Ecol. Evol. *6*, 1231–1238. https://doi.org/10.1038/s41559-022-01817-9.

40. Rudd, L., Packer, C., Biro, D., Firth, J.A., and Albery, G.F. (2024). Sex-Specific Social Ageing in Wild African Lions. Preprint, https://doi.org/10.2139/ssrn.4761072 https://doi.org/10.2139/ssrn.4761072.

41. Nussey, D.H., Coulson, T., Festa-Bianchet, M., and Gaillard, J.-M. (2008). Measuring senescence in wild animal populations: towards a longitudinal approach. Funct. Ecol. *22*, 393–406. https://doi.org/10.1111/j.1365-2435.2008.01408.x.

42. Ricklefs, R.E. (2008). The evolution of senescence from a comparative perspective. Funct. Ecol. *22*, 379–392. https://doi.org/10.1111/j.1365-2435.2008.01420.x.

43. Craft, M.E., Volz, E., Packer, C., and Meyers, L.A. (2011). Disease transmission in territorial populations: The small-world network of Serengeti lions. J. R. Soc. Interface *8*, 776–786. https://doi.org/10.1098/rsif.2010.0511.

44. Larson, S.M., Ruiz-Lambides, A., Platt, M.L., and Brent, L.J.N. (2018). Social network dynamics precede a mass eviction in group-living rhesus macaques. Anim. Behav. *136*, 185–193. https://doi.org/10.1016/j.anbehav.2017.08.019.

45. VanderWaal, K.L., Mosser, A., and Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Anim. Behav. *77*, 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028.

46. Elliot, N.B., Valeix, M., Macdonald, D.W., and Loveridge, A.J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions.

Oikos *123*, 1049–1056. https://doi.org/10.1111/oik.01266.

47. McDonald, J.L., Robertson, A., and Silk, M.J. (2018). Wildlife disease ecology from the individual to the population: Insights from a long-term study of a naturally infected European badger population. J. Anim. Ecol. *87*, 101–112. https://doi.org/10.1111/1365-2656.12743.

48. Stockmaier, S., Stroeymeyt, N., Shattuck, E.C., Hawley, D.M., Meyers, L.A., and Bolnick, D.I. (2021). Infectious diseases and social distancing in nature. Science *371*. https://doi.org/10.1126/science.abc8881.

49. Mbizah, M.M., Farine, D.R., Valeix, M., Hunt, J.E., Macdonald, D.W., and Loveridge, A.J. (2020). Effect of ecological factors on fine-scale patterns of social structure in African lions. J. Anim. Ecol. *89*, 2665–2676. https://doi.org/10.1111/1365-2656.13334.

50. Packer, C. (2023). The Lion: Behvaiour, ecology and conservation of an iconic species (Princeton University Press).

51. Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., and Sinclair, A.R.E. (2005). Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. Most, 390–393.

52. Pusey, A.E., and Packer, C. (1987). The Evolution of Sex-Biased Dispersal in Lions. Behaviour *101*, 275–310. https://doi.org/10.1163/156853987X00026.

53. Bygott, J.D., Bertram, B.C.R., and Hanby, J.P. (1979). Male lions in large coalitions gain reproductive advantages. Nature *282*, 839–841. https://doi.org/10.1038/282839a0.

54. Packer, C., Pusey, A.E., and Eberly, L.E. (2001). Egalitarianism in female African lions. Science *293*, 690–693. https://doi.org/10.1126/science.1062320.

55. Franks, D.W., Ruxton, G.D., and James, R. (2010). Sampling animal association networks with the gambit of the group. Behav. Ecol. Sociobiol. *64*, 493–503. https://doi.org/10.1007/s00265-009-0865-8.

56. Farine, D.R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. *84*, 1144–1163. https://doi.org/10.1111/1365-2656.12418.

57. Cairns, S.J., and Schwager, S.J. (1987). A comparison of association indices. Anim. Behav. *35*, 1454–1469. https://doi.org/10.1016/S0003-3472(87)80018-0.

58. Packer, C., Tatar, M., and Collins, A. (1998). Reproductive cessation in female mammals. Nature *392*, 807–811. https://doi.org/10.1038/33910.

59. Barthold, J.A., Loveridge, A.J., Macdonald, D.W., Packer, C., and Colchero, F. (2016). Bayesian estimates of male and female African lion mortality for future use in population management. J. Appl. Ecol. *53*, 295–304.

https://doi.org/10.1111/1365-2664.12594.

60. Packer, C. and, and Pusey, A.E. (1983). Adaptations of female lions to infanticide. Am. Nat. *121*, 716–728.

61. Blumstein, D.T., Wey, T.W., and Tang, K. (2009). A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc. R. Soc. B Biol. Sci. *276*, 3007–3012. https://doi.org/10.1098/rspb.2009.0703.

62. Fountain-Jones, N.M., Packer, C., Troyer, J.L., VanderWaal, K., Robinson, S., Jacquot, M., and Craft, M.E. (2017). Linking social and spatial networks to viral community phylogenetics reveals subtype-specific transmission dynamics in African lions. J. Anim. Ecol. *86*, 1469–1482. https://doi.org/10.1111/1365-2656.12751.

63. Craft, M.E. (2015). Infectious disease transmission and contact networks in wildlife and livestock. Philos. Trans. R. Soc. B Biol. Sci. *370*. https://doi.org/10.1098/rstb.2014.0107.

64. Riordan, P., Delahay, R.J., Cheeseman, C., Johnson, P.J., and Macdonald, D.W. (2011). Culling-Induced Changes in Badger (Meles meles) Behaviour, Social Organisation and the Epidemiology of Bovine Tuberculosis. PLoS ONE *6*, e28904. https://doi.org/10.1371/journal.pone.0028904.

65. Mysterud, A., Rauset, G.R., Van Moorter, B., Andersen, R., Strand, O., and Rivrud, I.M. (2020). The last moves: The effect of hunting and culling on the risk of disease spread from a population of reindeer. J. Appl. Ecol. *57*, 2509–2518. https://doi.org/10.1111/1365-2664.13761.

66. Munson, L., Terio, K.A., Kock, R., Mlengeya, T., Roelke, M.E., Dubovi, E., Summers, B., Sinclair, A.R.E., and Packer, C. (2008). Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. PLoS ONE *3*, 5–10. https://doi.org/10.1371/journal.pone.0002545.

67. Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofman-Lehmann, R., Lutz, H., et al. (1996). A canine distemper virus epidemic in Serengeti lions (Panthera leo). Nature *379*, 441–445. https://doi.org/10.1038/379441a0.

68. Mosser, A., and Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, Panthera leo. Anim. Behav. *78*, 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024.

69. Pusey, A.E., and Packer, C. (1994). Non-offspring nursing in social carnivores: Minimizing the costs. Behav. Ecol. *5*, 362–374. https://doi.org/10.1093/beheco/5.4.362.

70. Packer, C., Scheel, D., and Pusey, A.E. (1990). Why Lions Form Groups : Food is Not Enough Author. Am. Nat. *136*, 1–19.

71. Woodroffe, R., Donnelly, C.A., Cox, D.R., Bourne, F.J., Cheeseman, C.L., Delahay, R.J., Gettinby, G., McInerney, J.P., and Morrison, W.I. (2006). Effects of culling on badger Meles meles spatial organization: Implications for the control of bovine tuberculosis. J. Appl. Ecol. *43*, 1–10. https://doi.org/10.1111/j.1365-2664.2005.01144.x.

72. Shannon, G., Slotow, R., Durant, S.M., Sayialel, K.N., Poole, J., Moss, C., and McComb, K. (2013). Effects of social disruption in elephants persist decades after culling. Front. Zool. *10*, 62. https://doi.org/10.1186/1742-9994-10-62.

73. Nuñez, C.M.V., Adelman, J.S., and Rubenstein, D.I. (2015). Sociality increases juvenile survival after a catastrophic event in the feral horse (Equus caballus). Behav. Ecol. *26*, 138–147. https://doi.org/10.1093/beheco/aru163.

74. Testard, C., Larson, S.M., Watowich, M., Kaplinsky, C.H., Bernau, A., Faulder, M., Ruiz-Lambides, A., Higham, J.P., Montague, M., Snyder-Mackler, N., et al. (2020). Rhesus Macaques Build New Social Connections after a Natural Disaster. SSRN Electron. J., 1–11. https://doi.org/10.2139/ssrn.3741230.

75. Fedurek, P., McFarland, R., Majolo, B., and Lehmann, J. (2022). Social responses to the natural loss of individuals in Barbary macaques. Mamm. Biol. https://doi.org/10.1007/s42991-022-00283-x.

76. Houdt, S., Brown, R.P., Wanger, T.C., Twine, W., Fynn, R., Uiseb, K., Cooney, R., and Traill, L.W. (2021). Divergent views on trophy hunting in Africa, and what this may mean for research and policy. Conserv. Lett. *14*. https://doi.org/10.1111/conl.12840.

77. Packer, C., Funston, P., and Merwe, V.D. (2006). Impacts of Trophy Hunting on Lions in East and Southern Africa : Recent offtake and future recommen- dations. 11–13.

78. Hare, D., Dickman, A.J., Johnson, P.J., Rono, B.J., Mutinhima, Y., Sutherland, C., Kulunge, S., Sibanda, L., Mandoloma, L., and Kimaili, D. (2024). Public perceptions of trophy hunting are pragmatic, not dogmatic. Proc. R. Soc. B Biol. Sci. *291*, 20231638. https://doi.org/10.1098/rspb.2023.1638.

79. Dickman, A., Cooney, R., Johnson, P.J., Louis, M.P., and Roe, D. (2019). Trophy hunting bans imperil biodiversity. Science *365*, 874 LP – 874. https://doi.org/10.1126/science.aaz0735.

80. Mkono, M. (2022). How we can make the trophy hunting debate less fraught. Nat. Hum. Behav. *7*, 6–8. https://doi.org/10.1038/s41562-022-01488-3.

81. Loveridge, A.J., Valeix, M., Elliot, N.B., and Macdonald, D.W. (2017). The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. J. Appl. Ecol. *54*, 815–825. https://doi.org/10.1111/1365-2664.12794.

82. Heinsohn, R., and Packer, C. (1995). Complex Cooperative Strategies in Group-Territorial African Lions. Science *269*, 1260–1262.

https://doi.org/10.1126/science.7652573.

83. Scheel, D., and Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. Anim. Behav. *41*, 697–709. https://doi.org/10.1016/S0003-3472(05)80907-8.

# 3.9. Supplementary information

| Focal Sex | Response | Explanatory | Estimate | Lower | Upper | P |
|---|---|---|---|---|---|---|
| F | Strength.Female | Final year | -0.382 | -0.484 | -0.279 | <0.001 |
| F | Strength.Female | Penultimate year | -0.118 | -0.178 | -0.059 | <0.001 |
| F | Strength.Male | Final year | -0.334 | -0.465 | -0.202 | <0.001 |
| F | Strength.Male | Penultimate year | -0.034 | -0.112 | 0.043 | 0.385 |
| F | Degree.Female | Final year | -0.147 | -0.294 | -0.001 | 0.049 |
| F | Degree.Female | Penultimate year | -0.072 | -0.157 | 0.013 | 0.095 |
| F | Degree.Male | Final year | -0.194 | -0.376 | -0.012 | 0.036 |
| F | Degree.Male | Penultimate year | -0.066 | -0.174 | 0.042 | 0.228 |
| F | Mean Strength.Female | Final year | -0.402 | -0.571 | -0.234 | <0.001 |
| F | Mean Strength.Female | Penultimate year | -0.045 | -0.142 | 0.051 | 0.355 |
| F | Mean Strength.Male | Final year | -0.332 | -0.503 | -0.162 | <0.001 |
| F | Mean Strength.Male | Penultimate year | -0.047 | -0.146 | 0.052 | 0.355 |
| F | Groupsize | Final year | 0.294 | 0.099 | 0.489 | 0.003 |
| F | Groupsize | Penultimate year | 0.093 | -0.021 | 0.207 | 0.109 |
| M | Strength.Female | Final year | -0.182 | -0.383 | 0.020 | 0.076 |
| M | Strength.Female | Penultimate year | -0.127 | -0.263 | 0.008 | 0.066 |
| M | Strength.Male | Final year | -0.195 | -0.396 | 0.008 | 0.059 |
| M | Strength.Male | Penultimate year | 0.02 | -0.11 | 0.150 | 0.766 |
| M | Degree.Female | Final year | 0.011 | -0.217 | 0.240 | 0.926 |
| M | Degree.Female | Penultimate year | -0.106 | -0.256 | 0.045 | 0.167 |
| M | Degree.Male | Final year | 0.016 | -0.235 | 0.266 | 0.898 |
| M | Degree.Male | Penultimate year | 0.077 | -0.088 | 0.242 | 0.361 |
| M | Mean Strength.Female | Final year | -0.138 | -0.381 | 0.104 | 0.262 |
| M | Mean Strength.Female | Penultimate year | -0.08 | -0.238 | 0.078 | 0.322 |
| M | Mean Strength.Male | Final year | -0.217 | -0.455 | 0.021 | 0.073 |
| M | Mean Strength.Male | Penultimate year | -0.056 | -0.212 | 0.099 | 0.474 |
| M | Groupsize | Final year | 0.032 | -0.241 | 0.305 | 0.821 |
| M | Groupsize | Penultimate year | 0.024 | -0.163 | 0.210 | 0.804 |

**Table S1. Base model + SPDE effect estimates for the predictors of loss for both single sex models**. Table shows the penultimate and final year effects (“Explanatory” column) for each of the social metrics tested. “Focal Sex” indicates the model (F= female, M= male), “Response” indicates the response metric and target sex (e.g., Strength.Female = strength of associations to females from the focal sex).

| Focal Sex | Response | Explanatory | Estimate | Lower | Upper | P |
|---|---|---|---|---|---|---|
| F | Strength.Female | Strength to lost female | -0.062 | -0.105 | -0.019 | 0.004 |
| F | Strength.Female | Strength to lost male | -0.007 | -0.048 | 0.035 | 0.752 |
| F | Strength.Male | Strength to lost female | 0.023 | -0.033 | 0.078 | 0.428 |
| F | Strength.Male | Strength to lost male | -0.005 | -0.059 | 0.048 | 0.849 |
| F | Degree.Female | Strength to lost female | 0.005 | -0.057 | 0.067 | 0.881 |
| F | Degree.Female | Strength to lost male | -0.008 | -0.067 | 0.051 | 0.795 |
| F | Degree.Male | Strength to lost female | 0.066 | -0.01 | 0.142 | 0.088 |
| F | Degree.Male | Strength to lost male | 0.045 | -0.028 | 0.118 | 0.229 |
| F | Mean Strength.Female | Strength to lost female | -0.114 | -0.185 | -0.043 | 0.002 |
| F | Mean Strength.Female | Strength to lost male | -0.014 | -0.081 | 0.054 | 0.687 |
| F | Mean Strength.Male | Strength to lost female | -0.015 | -0.087 | 0.057 | 0.681 |
| F | Mean Strength.Male | Strength to lost male | -0.018 | -0.087 | 0.051 | 0.605 |
| F | Groupsize | Strength to lost female | -0.068 | -0.151 | 0.015 | 0.107 |
| F | Groupsize | Strength to lost male | -0.097 | -0.176 | -0.019 | 0.015 |
| M | Strength.Female | Strength to lost female | 0.023 | -0.087 | 0.134 | 0.687 |
| M | Strength.Female | Strength to lost male | 0.021 | -0.107 | 0.149 | 0.748 |
| M | Strength.Male | Strength to lost female | -0.001 | -0.109 | 0.106 | 0.980 |
| M | Strength.Male | Strength to lost male | 0.016 | -0.113 | 0.145 | 0.812 |
| M | Degree.Female | Strength to lost female | 0.097 | -0.028 | 0.222 | 0.130 |
| M | Degree.Female | Strength to lost male | -0.314 | -0.46 | -0.168 | <0.001 |
| M | Degree.Male | Strength to lost female | 0.035 | -0.1 | 0.17 | 0.614 |
| M | Degree.Male | Strength to lost male | -0.002 | -0.16 | 0.157 | 0.980 |
| M | Mean Strength.Female | Strength to lost female | -0.038 | -0.17 | 0.094 | 0.571 |
| M | Mean Strength.Female | Strength to lost male | 0.172 | 0.015 | 0.328 | 0.032 |
| M | Mean Strength.Male | Strength to lost female | 0.029 | -0.099 | 0.156 | 0.655 |
| M | Mean Strength.Male | Strength to lost male | -0.022 | -0.178 | 0.134 | 0.778 |
| M | Groupsize | Strength to lost female | -0.121 | -0.271 | 0.029 | 0.114 |
| M | Groupsize | Strength to lost male | -0.184 | -0.359 | -0.008 | 0.040 |

**Table S2. Base model + SPDE effect estimates for the response to loss for both single sex models**. Table shows the response to associate loss effects ("Explanatory" column) for each of the social metrics tested. "Focal Sex" indicates the model (F= female, M= male), "Response" indicates the response metric and target sex (e.g., Strength.Female = strength of associations to females from the focal sex).

| Focal Sex | Response | Explanatory | Estimate | Lower | Upper | P |
|---|---|---|---|---|---|---|
| F | Strength.Female | Age | -0.011 | -0.040 | 0.018 | 0.468 |
| F | Strength.Female | Longevity | -0.006 | -0.038 | 0.025 | 0.682 |
| F | Strength.Male | Age | 0.007 | -0.029 | 0.044 | 0.694 |
| F | Strength.Male | Longevity | 0.001 | -0.036 | 0.039 | 0.953 |
| F | Degree.Female | Age | 0.021 | -0.021 | 0.063 | 0.333 |
| F | Degree.Female | Longevity | 0.002 | -0.047 | 0.051 | 0.929 |
| F | Degree.Male | Age | -0.014 | -0.065 | 0.036 | 0.582 |
| F | Degree.Male | Longevity | 0.009 | -0.041 | 0.059 | 0.729 |
| F | Mean Strength.Female | Age | -0.056 | -0.104 | -0.008 | 0.023 |
| F | Mean Strength.Female | Longevity | -0.010 | -0.066 | 0.047 | 0.730 |
| F | Mean Strength.Male | Age | 0.038 | -0.009 | 0.086 | 0.116 |
| F | Mean Strength.Male | Longevity | -0.011 | -0.062 | 0.040 | 0.674 |
| F | Groupsize | Age | 0.047 | -0.008 | 0.102 | 0.092 |
| F | Groupsize | Longevity | 0.010 | -0.048 | 0.069 | 0.743 |
| M | Strength.Female | Age | 0.049 | -0.044 | 0.141 | 0.306 |
| M | Strength.Female | Longevity | -0.047 | -0.146 | 0.052 | 0.350 |
| M | Strength.Male | Age | -0.244 | -0.338 | -0.150 | <0.001 |
| M | Strength.Male | Longevity | 0.089 | -0.026 | 0.205 | 0.129 |
| M | Degree.Female | Age | 0.180 | 0.071 | 0.289 | 0.001 |
| M | Degree.Female | Longevity | 0.081 | -0.039 | 0.200 | 0.185 |
| M | Degree.Male | Age | -0.004 | -0.118 | 0.111 | 0.949 |
| M | Degree.Male | Longevity | 0.119 | 0.0003 | 0.237 | 0.049 |
| M | Mean Strength.Female | Age | 0.027 | -0.089 | 0.142 | 0.653 |
| M | Mean Strength.Female | Longevity | -0.116 | -0.251 | 0.019 | 0.092 |
| M | Mean Strength.Male | Age | -0.171 | -0.282 | -0.06 | 0.003 |
| M | Mean Strength.Male | Longevity | -0.044 | -0.184 | 0.095 | 0.533 |
| M | Groupsize | Age | 0.145 | 0.019 | 0.270 | 0.024 |
| M | Groupsize | Longevity | -0.057 | -0.189 | 0.076 | 0.398 |

**Table S3. Base model + SPDE effect estimates for ageing and longevity for both single sex models**. Table shows the ageing and lonegvity effects (“Explanatory” column) for each of the social metrics tested. “Focal Sex” indicates the model (F= female, M= male), “Response” indicates the response metric and target sex (e.g., Strength.Female = strength of associations to females from the focal sex).

**Figure S1. Spatial DIC changes.** DIC changes associated with fitting a spatial autocorrelation effect in our INLA models. More negative changes denote better-fitting models, and therefore more spatially autocorrelated social networks. Initial letters indicate the model (F= female, M= male), followed by the response metric and target sex (e.g., Strength.Female = strength of associations to females from the focal sex).

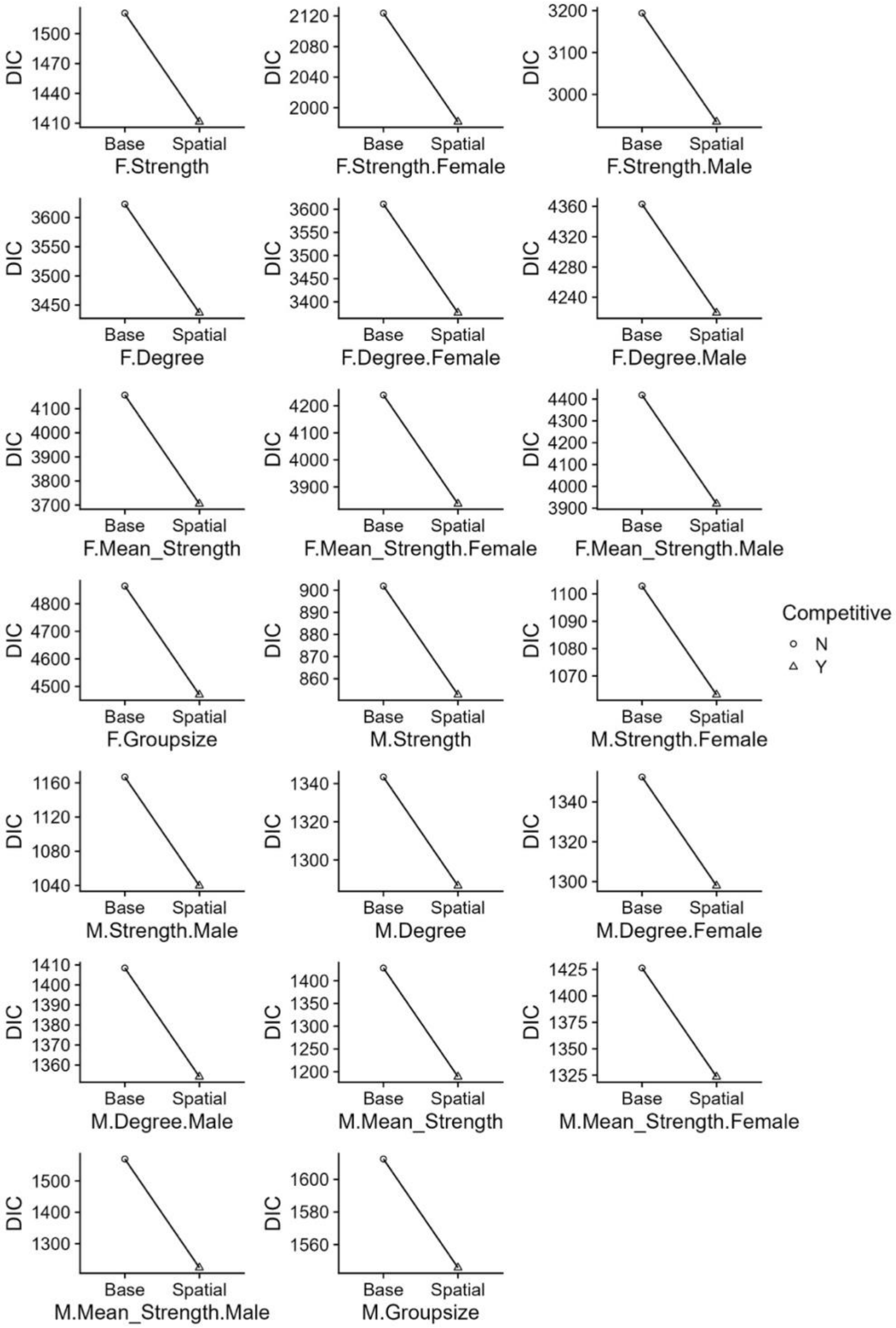


**Figure S2. $R^2$ values for final models.** Plots show the $R^2$ values, calculated by predicting values from the final models and correlating them with the observed values using Spearman's rank. Initial letters indicate the model (F= female, M= male), followed by the response metric and target sex (e.g., Strength.Female = strength of associations to females from the focal sex).

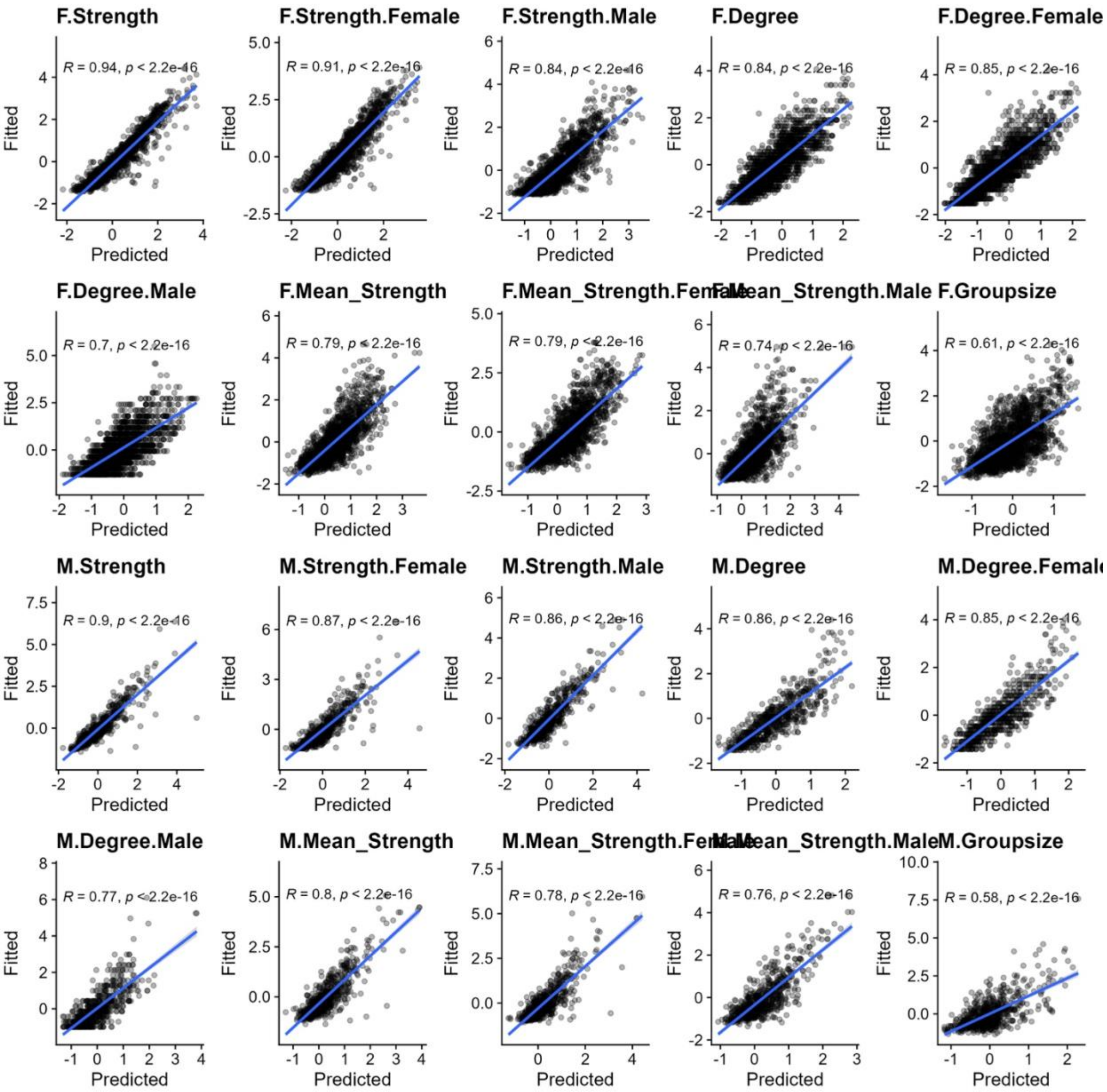
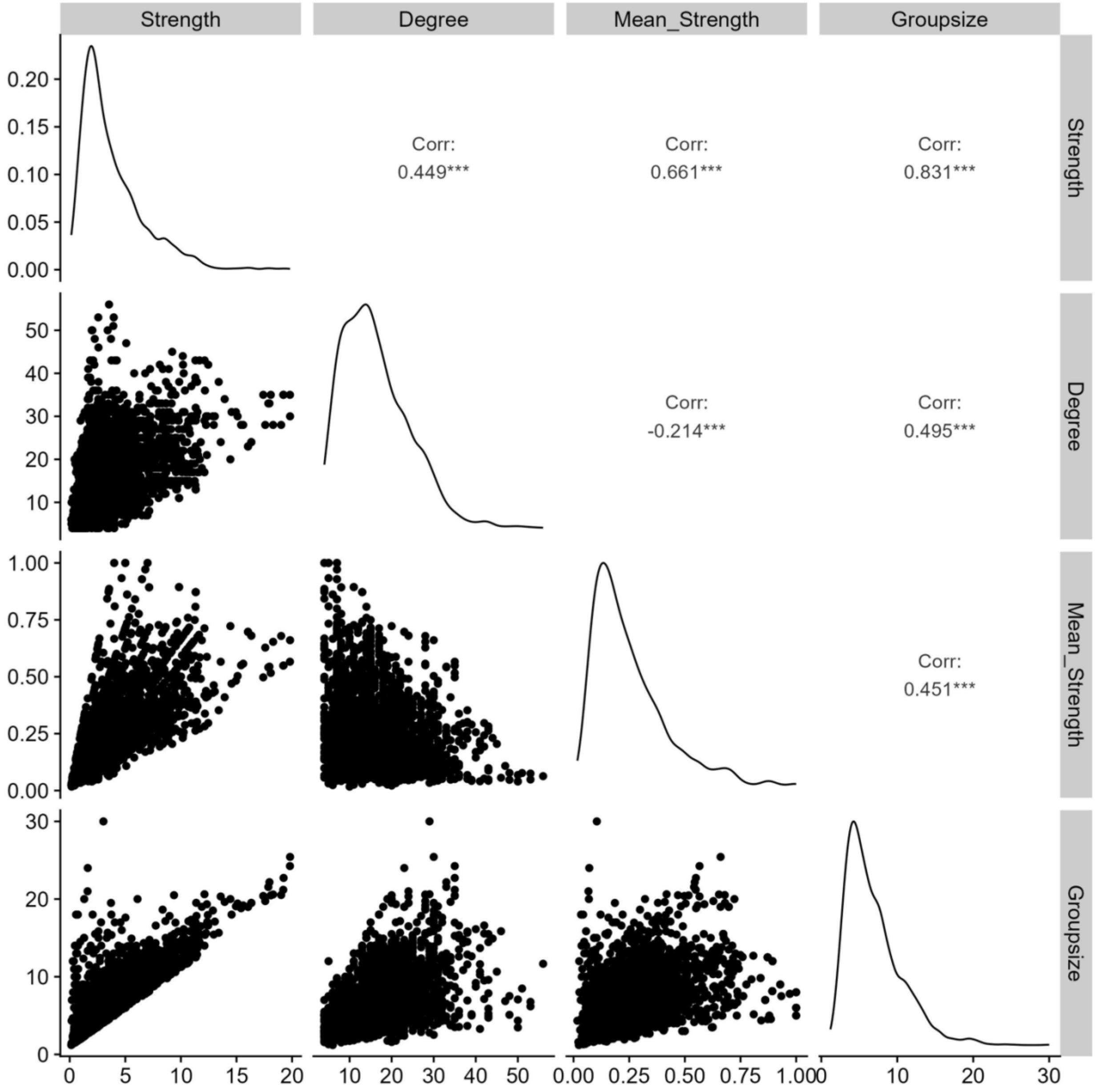


**Figure S3. Variabale correlation plots.** Pairwise plots depicting the correlations and associations between each of the included social network metrics. Pearson's statistic shown for each pair.



# 4. How identity-bias affects perceptions of conservation messages on social media

## 4.1. Abstract

Public support is essential for conservation, as public opinion can influence decision-making and policy. Therefore, understanding whether identity-bias against conservationists affects their perceived credibility and support for their recommendations is important. We conducted a vignette-style experiment to investigate the extent to which identity-bias influences the UK public's perceptions of African lion (*Panthera leo*) conservation messengers on X. We chose this focal species because of its global appeal and high public engagement in lion conservation discourse on social media. We created 24 fake X profiles with a pinned post about lion conservation and presented one profile to each of 1290 study participants (stratified to match the UK population regarding age, gender identity, and ethnicity). We held the lion conservation post constant across all profiles, but manipulated four experimental variables- the gender, race, expertise, and nationality of the messenger. We evaluated the effects of these variables on three response variables- respondents' perception of the credibility of post content, the

likelihood they would support implementing the lion conservation recommendation, and the trustworthiness of the messenger as a source of lion conservation information. Changing the experimental identity factors had varying impacts. Men were perceived to be communicating more credible lion conservation information than women. Support for implementing a stated lion conservation strategy was stronger when communicated by White professors than Black professors. Explicit trust in the character as a source of lion conservation information followed the same pattern. Additionally, there was an interaction effect of gender and race, with Black women perceived to be the least trustworthy. As such, our study highlights that bias against conservation messengers based on their identity may affect their credibility and uptake of their recommendations. Such bias is particularly concerning given the ongoing injustices and entrenched power inequalities in global conservation efforts.

## 4.2. Introduction

Many species are under threat, and effective conservation requires well-informed decision making[1,2]. However, conservation decisions and policy are not just based on ecological evidence: they are affected by the views of multiple publics, who may form their judgements based on different factors[3–5]. Public buy-in to conservation is vital [6] but can be contentious and challenging when the species of concern are highly valued and under substantial threat[7]. One such example is the African lion (*Panthera leo*).

The African lion is classed as vulnerable on the IUCN Red List, predominantly threatened by habitat fragmentation, conflict with people, and prey base depletion[8]. As such, strategies for conserving lion populations must balance the ecological needs of the species alongside the socio-economic dynamics of the landscapes within their range [9,10]. In particular, the success of future conservation efforts hinges on properly acknowledging and addressing colonial histories of Euro-centric conservation across lion ranges[11]. Globally the African lion holds immense cultural significance due to its high existence value[7], meaning that public engagement in the discourse around lion conservation is high even outside of its present range[12,13]. Given the complex and often controversial nature of lion conservation strategies, heated debates between stakeholders, scientists, policy makers and members of multiple publics - all with competing visions for how to best conserve lions - are frequent. While disagreements between scientists and stakeholders are often documented in academic publications[14–18], knowledge of debates within the public sphere (of any geographic location) are less well understood.

Much public discourse about lion conservation takes place on social media platforms such as X (formerly Twitter)[12,14,19], where the credibility of topical scientific information can be hard to establish[20], and the spread of misinformation is prolific[21]. As a consequence, debates can lack nuance and descend into verbal abuse directed towards those perceived to be “harming” wildlife[22], or become focused on division rather than finding mutually beneficial ways forward[23]. Often, such online public attention is dominated by publics in the Global North towards conservation action in the Global South with little consideration of local perspectives, such as in recent conversations around trophy hunting[13].

As conservation can depend on public donations and support, public opinion has real power to influence policy relevant decision-making and outcomes[22,24,25]. It is therefore critically important to understand whether and how, when discussing conservation recommendations on platforms such as X, bias towards individuals due to their identity (e.g., their race, gender; referred to from here on as “identity-bias”) impact their perceived credibility. Evidence of identity bias impacting behavior on social media has been observed in fields outside of conservation, where the gender and race of broadcasters impact their perceived objectivity by the public[26]. Similarly, the race and physical attractiveness of an individual’s profile photo has been found to impact public evaluations of trust in them, as well as the likelihood of following them[27].

The framing of a message can influence people's perceptions of environmental and conservation issues[28], as can the person delivering the message[29,30]. Therefore, it is important to understand how bias against certain voices (and their ideas) on social media platforms such as X might impact the direction of conservation resources and decision making. Ultimately this could influence outcomes for people, their livelihoods, and wildlife[19,31]. Such effects could be particularly damaging if compounded by conservation’s entrenched power inequalities, such as systematic prejudice against local communities and Indigenous peoples[32,33]. In addition, race and gender inequity within the professional conservation sphere[34–36] create a lack of visible diversity. Questions have been raised regarding the value placed on academic or scientific qualifications comparative to practical experience and contextual knowledge of conservation problems[37–40]. This can often be compounded by parachute science [41], when researchers from comparatively “rich” countries exploit the expertise and resources from “poorer” countries, and do not properly involve local collaborators. Taken together, these factors may create a stereotypical image in the public eye of what a ‘conservation expert’ looks like[42]. In turn, this could influence whose opinions are perceived as credible, and therefore trusted and supported, when debating contentious conservation issues online.

Here we report results from an online questionnaire experimentally investigating the effects of identity bias towards conservation messengers on X, amongst X users living in the UK (at the time of the study, the platform was branded as “Twitter”).  Specifically, we examined whether the race, nationality, gender, and level of expertise of those posting on X about lion conservation could influence i) perceived credibility of the lion conservation strategy they endorsed, ii) support for implementing that strategy, and iii) perceived trustworthiness of the source regarding lion conservation information. We evaluated whether and how identity bias impacts explicit perceptions of those sharing conservation messages, and the variation this generates in public engagement with such messaging. By identifying and quantifying such biases, we provide evidence to help rectify insidious problems of bias and inequity in global conservation efforts.

## 4.3. Methods

### 4.3.1. Questionnaire development and sampling

A group (n=8) of academics with expertise in conservation, human behavior, environmental justice, and equality, diversity and inclusion pre-tested our questionnaire, providing feedback on its clarity and relevance to the study aims. We incorporated their comments and suggestions into the questionnaire before data collection began. The final version of the questionnaire can be found in the supporting information (Appendix S1).

Using Qualtrics XM we recruited 1290 participants aged 18 and over living in the UK between Sept 6th and Nov 8th 2022 to respond to our survey, also hosted on the Qualtrics platform. To ensure our results were indicative of the adult UK population, we stratified our sample to match the most recently published statistics (at the time) on age, ethnicity, and gender identity[43] (Appendix S2). All respondents were financially compensated for their time.

### 4.3.2 Experimental Design

We created snapshots of fictitious Twitter profiles (now referred to as X profiles) from cover photo down to and including a pinned tweet (now referred to as a pinned post) using Inkscape. We manipulated the profile photo (sourced on Shutterstock), emojis and the language within the character’s biography to indicate their gender (man or woman), race (Black or White), nationality/location (Zimbabwe or UK), and expertise (Professor, Field

Assistant or Enthusiast- chosen to represent varied levels of knowledge, both formal and informal (Figure 1, see Appendix S3 for images of all profiles created). A full factorial design (2x2x2x3) resulted in 24 experimental conditions, each represented by a unique character embedded within the otherwise uniform image of a X profile. We took care when selecting the four different profile photos (to indicate man and woman, White and Black) to ensure characters appeared to be of a similar age and the photos were presenting the person in a similar way (directly facing the camera, smiling, visible from the shoulders up, and against a plain background). We used the name Pat Rogers for all characters.

While we expected the content of the lion conservation message to impact public perceptions of credibility, trustworthiness, and support, evaluating the effect of different messages was not our research objective. As such, we held the message constant. To determine which lion conservation message to use as the pinned post (to allow us to best interpret any effect of identity bias), we first conducted a preliminary message-selection study (see Appendix S3). Based on these results, the pinned post read *"If people are living in conflict with lions, those people must be relocated to protect lions and their habitats. We must keep lions safe from people at all costs."* and was held constant across all treatments. The questions were presented to all respondents in the same order, and they were unable to return to a previous question to change their answer. This allowed us to ensure that any effects of priming were uniform across all vignettes[44].

### 4.3.3. Procedure

Respondents first answered a block of socio-demographic questions to ensure they met the study quotas set for age, ethnicity, and gender identity, as well as a screening question about their X usage in the past 12 months. Any who did not fit the quotas and/or had not used X in the previous 12 months were not invited to continue. Next, respondents were presented with a short informative passage about lion conservation and management strategies (see Appendix S1). This was designed to be objective, provide context, and present an unbiased overview that ensured all respondents had sufficient information to answer the questionnaire. It was written in consultation with lion conservation researchers and based on published scientific information.

Each respondent was randomly assigned to one of 24 possible experimental conditions. The image of the X profile they were assigned remained visible throughout the portions of the questionnaire that it related to. Respondents answered three items measuring credibility, support, and trustworthiness using a seven-point Likert-type scale ranging from “strongly disagree” to “strongly agree”, with a midpoint of “neither agree nor disagree” and an additional “I don’t know” option.

To measure perceived credibility, support for the recommendation, and perceived trustworthiness, we asked:

1. To what extent do you agree that the information presented in Pat Rogers' pinned post is credible? (measuring credibility)

2. To what extent do you agree with Pat Rogers that we should relocate people to address human-lion conflict? (measuring support)
3. To what extent do you agree that Pat Rogers is a trustworthy source of lion conservation information? (measuring trustworthiness)

Participants then provided information on their level of X usage, level of formal education, the extent to which they support human rights and animal rights, how they would prioritize the interests of people versus the interests of wild animals when their interests clash [24], and how much confidence they have in scientists to act in the best interests of the public. The full questionnaire is available in Appendix S1.

The study received ethics clearance by a subcommittee of the University of Oxford Central University Research Ethics Committee (R79948/RE001), and all respondents provided informed consent prior to answering any questions.

### 4.3.4. Data Analysis

We analysed data using R version 4.2.0. A detailed breakdown describing the sample, including demographic characteristics and covariates, can be found in Appendix S2. The median response time was 176.5 seconds, and we removed all responses from participants who took less than half, or more than four times the median prior to analysis, giving n=1290). Respondents who answered “I don’t know” to one or more of the three questionnaire items measuring credibility, support and trustworthiness were removed prior to conducting the analysis for that question. The resultant sample sizes were, n =

1254 responses for question 1, n = 1260 responses for question 2, and n = 1178 for question 3. We used the likert package[45] to visualize raw data.

Using the ordinal package[46], we fitted separate ordinal logistic regression models to quantify relationships between the experimental factors manipulated within the vignettes (gender, race, nationality, and expertise) and credibility, support and trustworthiness. All appropriate model assumption tests were satisfied. For each analysis, we first fitted a global model containing all experimental factors and all possible interactions between these factors, as well as respondents' age, gender identity, ethnicity, extent of X usage, how much confidence they have in scientists to act in the public's interest, the extent to which they support human rights and animal rights, and how they would prioritize the interests of wild animals versus people. Owing to the low number of participants identifying with certain ethnicities, all responses were condensed into broader ethnicity categories of White, Asian/Asian British, Black/African/Caribbean/Black British, Mixed/multiple ethnic groups, Other ethnic groups, and prefer not to say, in line with the classification system used by the Office for National Statistics in the United Kingdom[43] (Appendix S2).

Using the MuMIn package[47] we compared corrected Akaike information criterion ($AIC_c$) values for each global model and all possible nested models within it. The top-supported model for each response variable was identified as that with the lowest $AIC_c$. After removing uninformative and redundant parameters[48,49], we calculated $AIC_c$ weights for top-supported models (Appendix S4). We report parameter estimates alongside 85%

Confidence Intervals (CIs) (Appendix S5, S6.1, and S7.1), as is best practice for model selection using information theory, to ensure model-selection and parameter-evaluation criteria are congruent[48,50]. We include both 85% and 95% CIs in all figures to facilitate easy visual comparison with more commonly understood CIs [50]. We conducted post-hoc Tukey tests using the emmeans package[51] to evaluate the effects of each level of our predictor variables within the interaction terms (Appendix S6.2 and S7.2). We used ggplot2[52] to visualize these interactions, and the coefficient estimates for the predictors in each top-supported model.

## 4.4. Results

### 4.4.1. Credibility of the pinned post

Agreement with the credibility of Pat Rogers' pinned post varied depending on the character presented (Figure 2a). Our top-supported model of credibility ($AIC_c$ weight = 0.22, Appendix S4.1) contained a main effect of one experimental factor, the gender of Pat Rogers. Holding all other predictors constant, respondents were more likely to agree that the pinned post was credible if it was embedded within a man's profile than a woman's profile (log odds ratio [SE] = 0.157 [0.103], see Figure 2b and Appendix S5).

The model also contained effects of the respondent’s support for animal rights, support for human rights, beliefs about whether to prioritize people or animals, the extent of their trust in scientists, level of X usage, their age, and ethnicity (Appendix S5). Respondents who strongly supported animal rights were more likely to agree that the pinned post was credible (log odds ratio [SE] = 3.636 [0.925]). Conversely, respondents were less likely to agree that the pinned post was credible if they strongly prioritized people over animals (log odds ratio [SE] = -1.207 [0.224]). In addition, respondents that had a great deal of trust in scientists to act in the public interest were more likely to agree that the pinned post was credible compared to those who had no trust at all (log odds ratio [SE] = 1.255 [0.338]). Those who used X daily were also more likely to agree that the pinned post was credible compared to those who used it less than once a month (log odds ratio [SE] = 0.454 [0.212]). Older respondents were less likely to agree that the pinned post was credible (log odds ratio [SE] = -0.01 [0.003]; Figure 2b, Appendix S5).

Despite being in the model, the relationship between respondents' agreement with the credibility of the pinned post and their support for human rights was not straightforward to interpret. This was also true of the relationship with respondents' ethnicity. In both cases this was likely due to small numbers of respondents in some of the categories included (Figure 2b, Appendices S2 and S5).

### 4.4.2. Support for position taken (relocating people)

Support for the character’s stated position (in this case relocating people to address human-lion conflict) varied depending on the character sharing the message (Figure 3a).

The top-supported model ($\mathrm{AIC_c}$ weight = 0.35, Appendix S4.2) contained two experimental factors, the race and expertise of Pat Rogers, and the interaction between these factors. Holding all other predictors constant, respondents were more likely to support relocating people when the message came from a Black character rather than a White one (log odds ratio [SE] = -0.300 [0.179]). Pat Rogers's expertise affected support for relocating people to protect lions. Contrary to expectation, people were more likely to support relocation when it was shared by an enthusiast when compared to a field assistant (log odds ratio [SE] = -0.214 [0.174]) or to a professor (log odds ratio [SE] = -0.437 [0.177]; Figure 3b and Appendix S6.1).

However, the influence of expertise depended on race. When Pat Rogers was Black, respondents were most likely supportive of people's relocation if they were an enthusiast (Tukey test, estimate [SE] = 1.076 [0.127]), followed by a field assistant (Tukey test, estimate [SE] = 0.862 [0.125]), and were least likely to support a professor (Tukey test, estimate [SE] = 0.639, [0.127]). In contrast, when Pat Rogers was White, the order was reversed: support for relocating people was highest when Pat was a professor (Tukey test, estimate [SE] = 1.066, [0.126]), followed by an enthusiast (Tukey test, estimate [SE] = 0.776, [0.132]), and lowest for a field assistant (Tukey test, estimate [SE] = 0.586, [0.127]; see Figure 4a and Appendix S6.2).

In addition, the top-supported model contained effects of respondents' support for animal rights and human rights, their beliefs about the prioritization of people versus animals, the extent of their trust in scientists, their level of X usage, their age, and their ethnicity. These factors were all similarly contained in the top-supported model for the perceived credibility of the pinned post, and the relationships between the levels of these factors and support for relocating people was near identical to those outlined in section 3.1 (all log odds ratios and SE are available in Appendix S6.1).

### 4.4.3. Trustworthiness of Pat Rogers

Agreement that Pat Rogers was a trustworthy source of lion conservation information varied depending on the character presented (Figure 5a). The top-supported model ($AIC_c$ weight = 0.23, Appendix S4.3) contained three of the experimental factors, the race, gender, and expertise of Pat Rogers, as well as the two-way interactions between race and expertise, and race and gender. Holding all other predictors constant, respondents were more likely to agree that Pat Rogers was a trustworthy source of lion conservation information if they were Black rather than White (log odds ratio [SE] = -0.012 [0.216]), and if they were a man rather than a woman (log odds ratio [SE] = 0.320 [0.149]). Pat Rogers's expertise did not increase trustworthiness. Respondents were more likely to trust Pat Rogers when they were an enthusiast as compared to a field assistant (log odds ratio [SE] = -0.112 [0.181]) or a professor (log odds ratio [SE] = -0.116 [0.185]; Figure 5b and Appendix S7.1).

However, the extent of trust in Pat Rogers' expertise was dependent on their race. Professor was the most trusted expertise level when Pat Rogers was White (Tukey test estimates [SE] = 1.504, [0.137]), but least trusted when they were Black (Tukey test estimates [SE] = 1.160, [0.137]). Conversely the enthusiast was perceived as the most trustworthy when Pat Rogers was Black (Tukey test estimates [SE] = 1.276, [0.136]), but the least trustworthy when they were White (Tukey test estimates [SE] = 0.974, [0.137]; Figure 4b). Trust of the Black field assistant and White field assistant sat in the middle (Tukey test estimates [SE] = 1.164, [0.132] and 1.075, [0.137] respectively)

The influence of gender on respondents' trust in Pat Rogers was further dependent on Pat Rogers' race. When Pat Rogers was a man, they were perceived as more trustworthy when they were Black (Tukey test, estimate [SE] = 1.359, [0.114]) than when they were White (Tukey test, estimate [SE] = 1.060, [0.111]). However, the opposite was true when Pat Rogers was a woman, with respondents perceiving the White character as more trustworthy than the Black character (Tukey test, estimates [SE] = 1.315, [0.118] and 1.038, [0.111] respectively; Figure 4c and Appendix S7.2).

The demographic and social identity factors in the top-supported model included extent of support for animal rights, their beliefs about the prioritization of people versus animals, their extent of trust in scientists, level of X usage, and ethnicity. The relationships between the levels of these factors and agreement that Pat Rogers was a trustworthy source of lion conservation information was near-identical to those in the previous models as discussed in sections 3.1 and 3.2 (all log odds ratios and SE are available in Appendix S7.1).

## 4.5. Discussion

We evaluated whether and how identity bias impacts explicit perceptions of those speaking about conservation, and the variation this generates in public engagement with lion conservation messaging, on X. Across a sample stratified to approximate the UK public, we found evidence that identity-bias influenced the perceived credibility of lion conservation information, support for acting on that information, and the trustworthiness of a conservation messenger. Specifically, we found bias relating to the race, gender, and expertise of the conservation messenger, but not their nationality. This could be due to the lack of immediate visibility of the character's nationality in the profiles created, as it was indicated via a small flag emoji in the profile biography, and the location tag.

Overall, men were perceived to have posted more credible lion conservation information than women. However, gender did not explain support for implementing the conservation strategy in the pinned post. Gender bias, its impact within the field of conservation, and recommendations for addressing such inequities, have been well documented in the literature[34,53–56]. On X, research has found that women in other scientific fields have fewer followers, reposts and likes compared to men[57]. This relationship is also found in the Altmetric scores of papers, with higher scores attributed to those published with lead authors who are men versus women[58]. Here, we evidenced the nuances of such gender bias in conservation discourse on X. While the public perceived women as less credible when discussing conservation, this bias did not significantly affect public support for their recommendations.

Further, when broken down by race, we found that White women were perceived as more explicitly trusted sources of lion conservation information than White men, even though men were perceived to have posted more credible information. This contrasted with Black men being perceived as more trustworthy than Black women regarding lion conservation information (see Figure 4b for more detail, but from highest to lowest perceived trustworthiness were Black man, White woman, White man, Black woman). This highlights the importance of using an intersectional lens when examining patterns of bias in conservation[59,60]. The devaluing of Black women's opinions and expertise, combined with inflated workloads comparable to their White colleagues in academia, have been well documented[61–63]. It is possible that chronic devaluation, combined with racial stereotyping (related to inferred nationality and presumptions of local knowledge, which is discussed later in this section), are driving the observed gender-race interaction patterns.

Men use stronger language to promote the importance of their scientific research than do women[64]. By holding the message we used constant across all treatments, the results demonstrated that bias against women speaking about conservation exists irrespective of the way in which they convey their opinion. Our results indicate a need to consider the potential for additional impacts of gender bias on public perceptions of messengers on social media, such as funding distribution and public engagement opportunities[65], including how these might interact with race and the conservation context presented. In this study only binary gender was used, but conducting similar studies using a greater spectrum of gender identities would further enrich our understanding.

We found no effect of expertise, indicated by a professional title, on the perceived credibility of conservation information shared via a post on X. While surprising, it suggests that rejections of conventional scientific expertise are prolific on X, which aligns with the well-documented abundant and rapid spread of science misinformation on social media platforms[21]. It could also be indicative of an increasing public acknowledgement and recognition of multiple "ways of knowing" outside of formally qualified experts [38–40]. However, we did find an effect of the interaction between the expertise and race of the messenger on both support for relocating people to protect lions, and the character's perceived trustworthiness. The White professor received considerably more support and trust than the Black professor. Furthermore, the Black professor was both the least supported and trusted when compared to the Black field assistant and enthusiast, while the White professor was consistently the most supported and trusted compared to the White field assistant and enthusiast.

These findings likely stem from societal racism and stereotypical conceptions of what an "expert" in conservation looks like amongst the UK public[42]. This is particularly likely given the low Black representation amongst senior academics, and so professors, in UK higher education institutions[66]. Our results highlight potential real-world implications of this, with the societal prestige of a White professor not afforded equally to those who are Black. Additionally, our results may reflect public exposure to biased conservation narratives in popular media, which often center White individuals as the "scientific experts"[13,67,68].

It is possible that the greater support for and trust in Black enthusiasts and field assistants, compared to White enthusiasts and field assistants, was due to assumptions about the superior contextual understanding that Black messengers had of lion conservation due to their inferred nationality. We varied nationality across all the X profiles and did not detect an effect, but this could have been because racial stereotypes superseded the way we signaled nationality. To investigate, further research could explicitly test intersectional identity dynamics by signaling nationality more clearly. It would further be interesting to examine how support varies based on the inferred location of the conservation issue being discussed, and the race of the person discussing it. Additionally, it would be valuable to examine any impacts of racial affinity bias (in favour of individuals we perceive to be "like us"[69] between each respondent and the messenger based on shared identity. This would require a larger sample size of respondents from minority ethnicities, rather than a respondent pool stratified to match the ethnic demographics of the adult UK population.

Combined, our findings warrant serious consideration given the ability for public opinion to sway conservation policy and funding decisions[25,70,71]. For example, in the situation we presented, racial bias towards conservation messengers impacted support for a conservation action (relocating people to protect lions) that would likely have serious human rights and livelihood consequences for local communities. As such, this study builds on existing knowledge of racism in conservation[35,72,73], by highlighting the links between public perceptions of expertise, and conservations' history of oppression, entrenched discrimination, and White western centered narratives.

When considering participants' social identities, the extent of support for animal rights had the biggest impact on responses across all three research questions. Namely, greater support for animal rights increased the perceived credibility of information in the post, extent of support for relocating people to protect lions, and the perceived trustworthiness of the messenger. A similar pattern was observed across all questions for participants who reported that they would prioritize wild animals over people if their interests clashed. Given that the embedded message was heavily skewed towards an animal-centered as opposed to a people-centered solution to human-wildlife conflict (Appendix S3), these patterns were expected. The magnitude of these effects suggests orientations around animal rights support have significant potential to influence how the public view not only conservation strategies, but also the credibility of those discussing conservation on X. Other research has shown comparable trends when examining the relationship between individuals' social identities and their perspectives on contentious conservation scenarios [24,74,75]. It is therefore important that the potential for inherent beliefs to overshadow objectivity are considered, especially when public opinion on conservation issues could influence decision making and the direction of funds[19].

It is harder to interpret the pattern between participants' support for human rights, the credibility they attached to the suggestion of relocating people to protect lions, and their inclination to support doing so. Only a small proportion of respondents didn't support human rights (n=17, somewhat disagree to strongly disagree). If we only consider participants who did support human rights, we see a trend that increasing agreement (from neutral to strongly agree) resulted in a decrease in perceived credibility and support for their recommendations (Figures 2b, 3b). This is as expected given that the post advocates for a strategy that is likely to infringe on both human and land rights, highlighting the importance of accounting for nuances in individuals' beliefs when considering their interactions with conservation information. When confronted with complex and controversial conservation problems, social identities have been shown to impact public opinion in multiple scenarios[24,76–78]. Our results add to these findings and highlight the need to consider not only how identity-politics can influence public opinion of conservation problems, but also those sharing conservation messages.

Participants who were less trusting of scientists to act in the best interest of the public expressed weaker agreement across all research questions, suggesting general mistrust of scientists can influence perceptions of conservationist messengers regardless of their expertise. We chose to ask this question broadly, despite scientists being a non-homogenous group, to facilitate evaluation of an overall measure of trust. The concept of "trust" in scientists is a complex area of research[79], and our results echo others that advocate for the consideration of these dynamics when engaging the public with science, particularly in concert with individuals' political ideology[80,81]. Additionally, participants who used X more frequently were more agreeable across all research questions. There is likely a reduced skepticism of conservation information and those sharing such messages on X that comes with increased use of the platform. It should again be noted that this study was conducted before "Twitter" was rebranded as "X" and lost a lot of scientific users[82], so this will not have impacted the results.

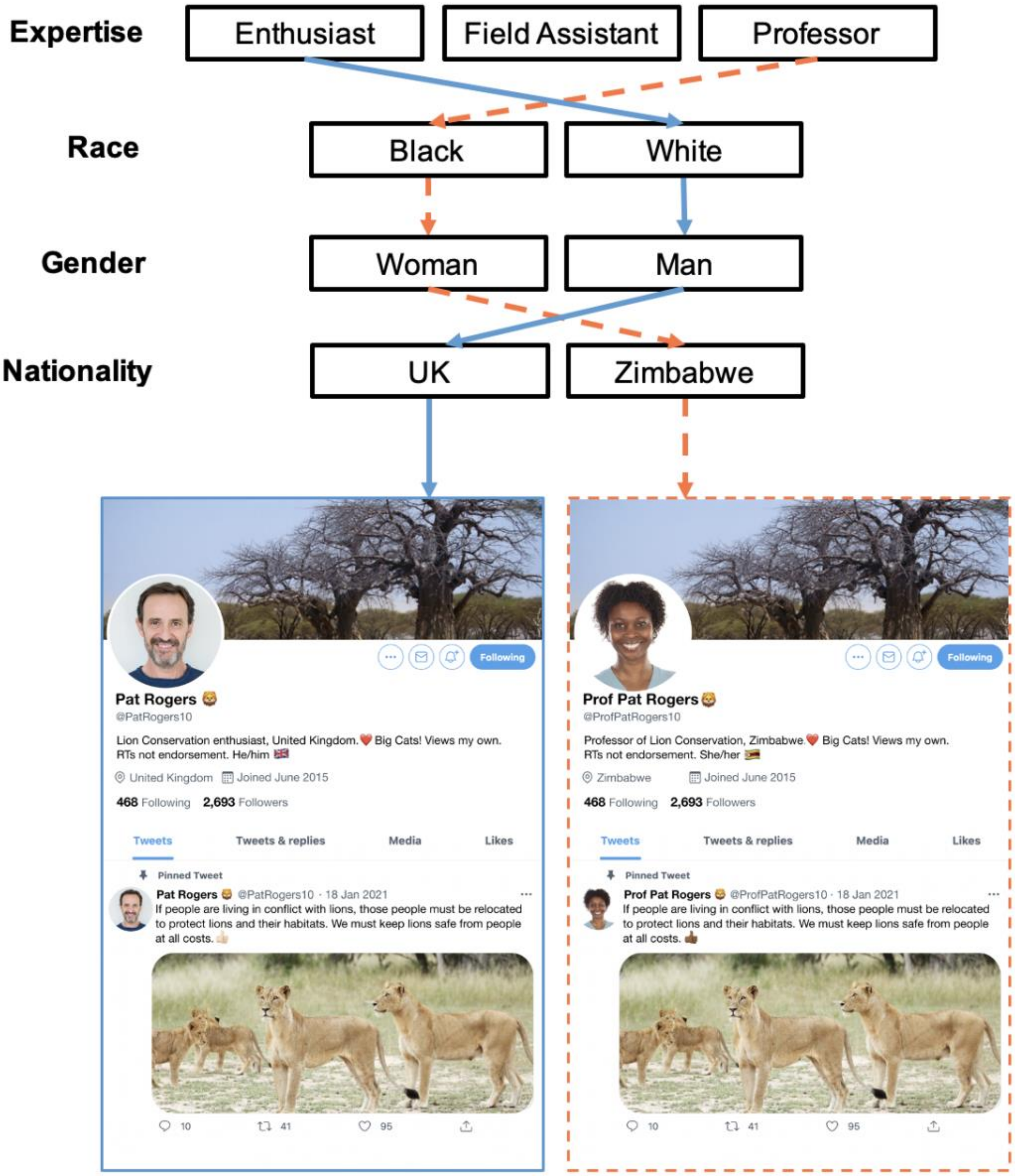
Overall, we found subtle differences in the impact of identity on each of the metrics we tested (Appendix S8). Men were perceived to be communicating a more credible lion conservation strategy than women, but gender had no effect on support for implementing that strategy. Instead, it was the interaction between the messenger's race and expertise that was relevant. White professors generated more support for relocating people to protect lions than White enthusiasts or field assistants. Conversely, Black professors generated less support than Black enthusiasts or field assistants. Finally, explicit trust in the messenger was impacted by the interaction between the messenger's gender and race, as well as their expertise and race. Most prominently, White professors were perceived as more trustworthy than any other messenger.

We restricted the identity factors and levels examined to those most intuitively relevant to the context of the study, to avoid statistically uninterpretable results. However, there are numerous other identity biases both within conservation and more broadly in society (e.g., sexuality, religion, disability), which would be valuable to explore in future studies. A deeper examination of geographic biases, particularly regarding racial stereotypes, nationality, and the contextual location of the conservation situation presented would also be of interest. As an example, comparing these results to a study contextualized within a British conservation problem (e.g., strategies to reduce human-badger conflict[83]) may clarify queries around the potential effects of racial stereotyping as a proxy for perceived local knowledge of conservation issues. Furthermore, testing identity biases of publics outside of the UK could provide additional insights for comparison, and may influence the effects of the gender and race of the conservation messenger dependent on contextual dynamics within the country. Examining these dynamics amongst those working within conservation advocacy groups and funding bodies could also prove interesting, as we might expect they would place more value on an individuals' expertise than the public. In addition, it would be valuable for future studies to consider varying the content of the message itself. Specifically, testing controversial messages (such as permitting trophy hunting, see Appendix S3.4) against messengers we found to generate high versus low public trust, would facilitate an understanding of whether stances on particularly contentious topics can sway public opinion of a conservation messenger.

While we found that respondents' social identities and beliefs had the strongest influence on all outcomes, even when accounting for these, the identity of the messenger mattered. Our results demonstrate that public interaction with conservation information is not objective and is influenced by inherent biases, as has been observed in several other fields [26,84,85]. Perhaps most alarming is the finding that in these hypothetical examples, the voice of experts in the field (professors and field assistants in this study) are viewed differently by virtue of their race - following long documented past and present patterns of discrimination and oppression within conservation[35,72]. Not only does this suggest the potential for real-world impacts on conservation outcomes based on identity bias, but also raises questions about the dangers of homogenous ideas proliferating within conservation spaces owing to the reduced diversity of voices being heard [86].

Despite increased attention towards these issues within the field of conservation over recent years, action is still limited and slow. Our results add further fuel to the drive towards addressing these injustices, and specifically calls for increased communication about such biases within conservation to wider stakeholders such as the public, decision makers, politicians, and funders. Conservation as a field relies upon vast and varied groups, all of whom carry their own set of biases and preconceived ideas about who a conservation ‘expert’ is. While these results could be used to advocate for manipulating conservationists’ identity-factors advantageously when communicating recommendations, this would be highly unethical. Instead, we argue that it is only by collectively taking responsibility for ensuring parity, and platforming diverse voices, that such biases and misconceptions can be rectified. This will ultimately build a more just, equitable and effective conservation arena *(see Appendix S9 for extended results and discussion).*

## 4.6. Figures



**Pat Rogers** 🦁
@PatRogers10

Lion Conservation enthusiast, United Kingdom.❤️ Big Cats! Views my own.
RTs not endorsement. He/him 🇬🇧

United Kingdom Joined June 2015

468 Following 2,693 Followers

**Pat Rogers** 🦁 @PatRogers10 · 18 Jan 2021
If people are living in conflict with lions, those people must be relocated to protect lions and their habitats. We must keep lions safe from people at all costs. 👍🏻

**Prof Pat Rogers** 🦁
@ProfPatRogers10

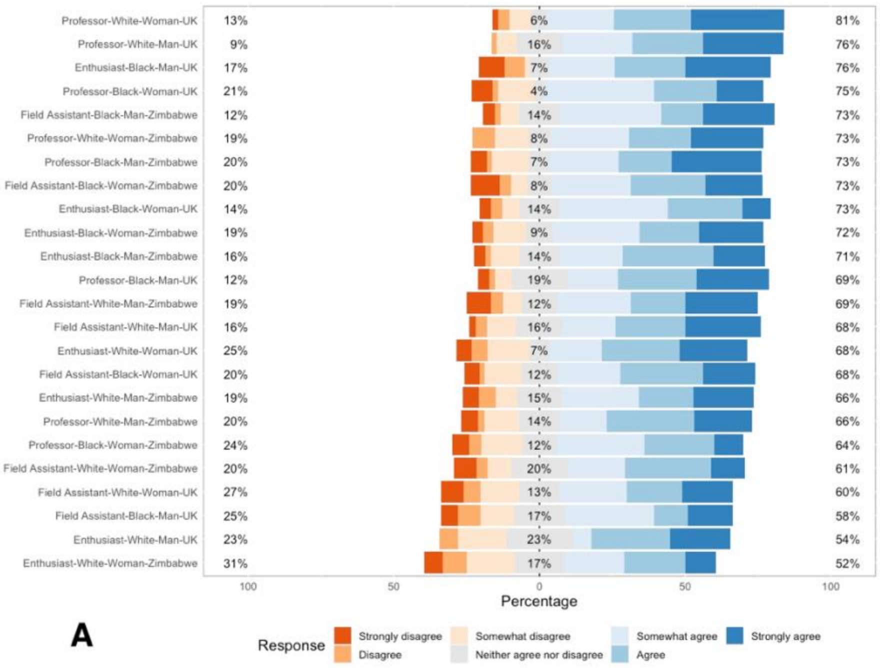
Professor of Lion Conservation, Zimbabwe.❤️ Big Cats! Views my own.
RTs not endorsement. She/her 🇿🇼

Zimbabwe Joined June 2015

468 Following 2,693 Followers

**Prof Pat Rogers** 🦁 @ProfPatRogers10 · 18 Jan 2021
If people are living in conflict with lions, those people must be relocated to protect lions and their habitats. We must keep lions safe from people at all costs. 👍🏿

**Figure 1. Diagram outlining the experimental design, with two example profiles shown.** All snapshots (X profile + pinned post) were identical apart from the specifics related to each factor we manipulated. Expertise was demonstrated using the text in the biography and the presence/absence of Prof before the name; race was demonstrated via the profile image and the color of the thumbs up emoji in the pinned post; gender was demonstrated using the profile image and the pronouns in the biography; nationality was demonstrated using the text and the flag emoji in the biography, and the location tag. 24 profiles were created in total by combining the levels shown in a fully factorial design (Appendix S3).



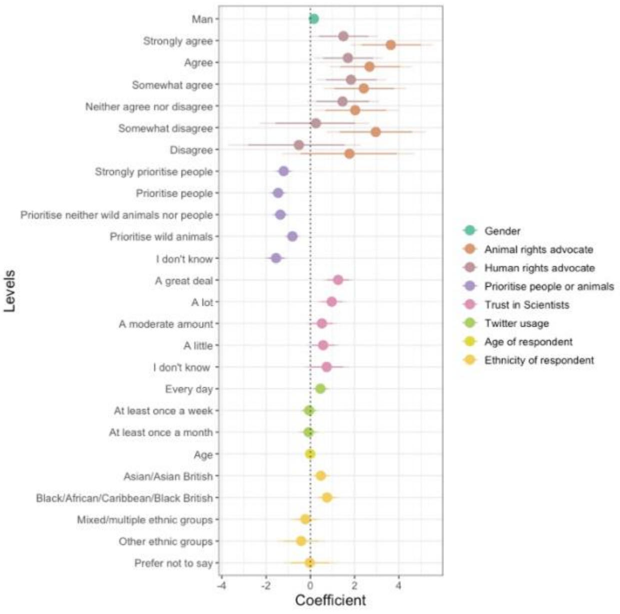
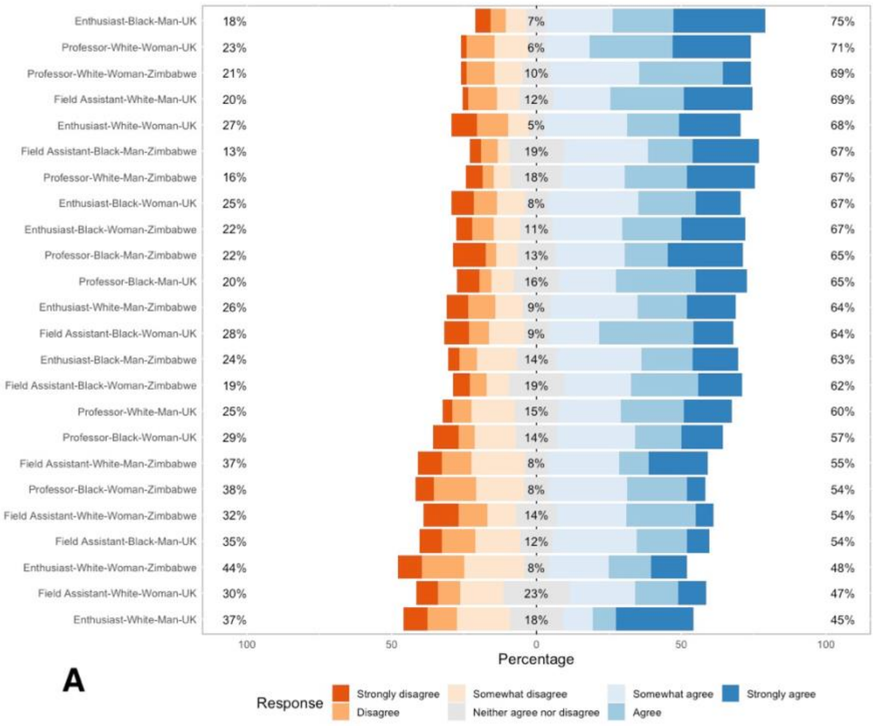


**Figure 2a. Agreement that the information in Pat Rogers' pinned tweet is credible, grouped by the experimental profile presented as expertise/race/gender/nationality.** Each bar represents the responses to one of the 24 profiles being tested, and shows the distribution of responses, coloured from reds (disagreement), through grays (neutrality) to blues (agreement). The percentage figures show the number of respondents who overall disagreed (left), were neutral (middle) or agreed (right), after excluding "I don't know" responses.

**Figure 2b. Directional associations between agreement that Pat Rogers pinned tweet is credible and the variables in the top-supported model.** Points indicate the log-odds ratios (or coefficient estimates) for the levels of each variable (shown in the key on the right hand side) relative to the reference category for categorical variables (gender = woman; animal rights advocate & human rights advocate = strongly disagree; prioritise people or animals = strongly prioritise wild animals; trust in scientists = no confidence; twitter usage = less than once a month; ethnicity = English/Welsh/Scottish/Northern Irish/British). Positive coefficients demonstrate increased agreement comparative to the reference level, while negative coefficients demonstrate decreased agreement. Coloured error bars show the 85% CIs, with transparent error bar extensions indicating the 95% CIs.



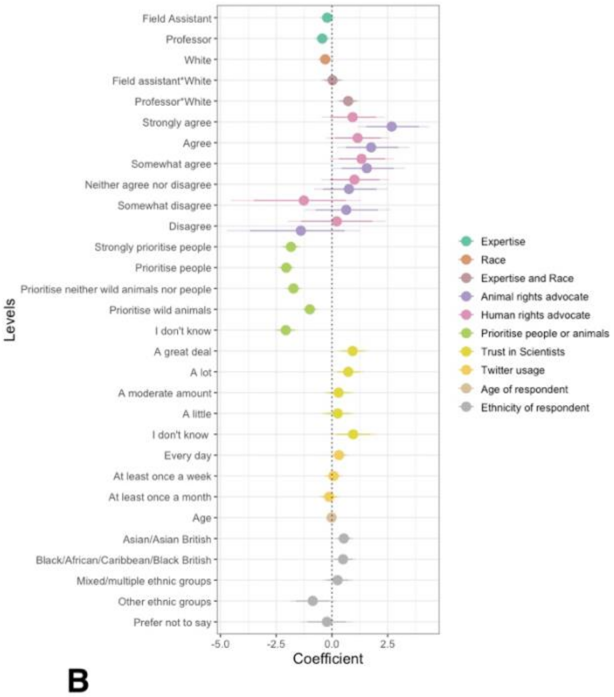


**Figure 3a. Extent of agreement with Pat Rogers that we should relocate people to protect lions, grouped by the experimental profile presented as expertise/race/gender/nationality.** Each bar represents the responses to one of the 24 profiles being tested, and shows the distribution of responses, coloured from reds (disagreement), through greys (neutrality) to blues (agreement). The percentage figures show the number of respondents who overall disagreed (left), were neutral (middle) or agreed (right), after excluding "I don't know" responses.

**Figure 3b. Directional associations between agreement with Pat Rogers that we should relocate people to protect lions, and the variables in the top-supported model.** Points indicate the log-odds ratios (or coefficient estimates) for the levels of each variable (shown in the key on the right hand side) relative to the reference category (expertise = enthusiast; race = Black; animal rights advocate & human rights advocate = strongly disagree; prioritise people or animals = strongly prioritise wild animals; trust in scientists = no confidence; twitter usage = less than once a month; ethnicity = English/Welsh/Scottish/Northern Irish/British**.** Positive coefficients demonstrate increased agreement comparative to the reference level, while negative coefficients demonstrate decreased agreement. Coloured error bars show the 85% CIs, with transparent error bar extensions indicating the 95% CIs.

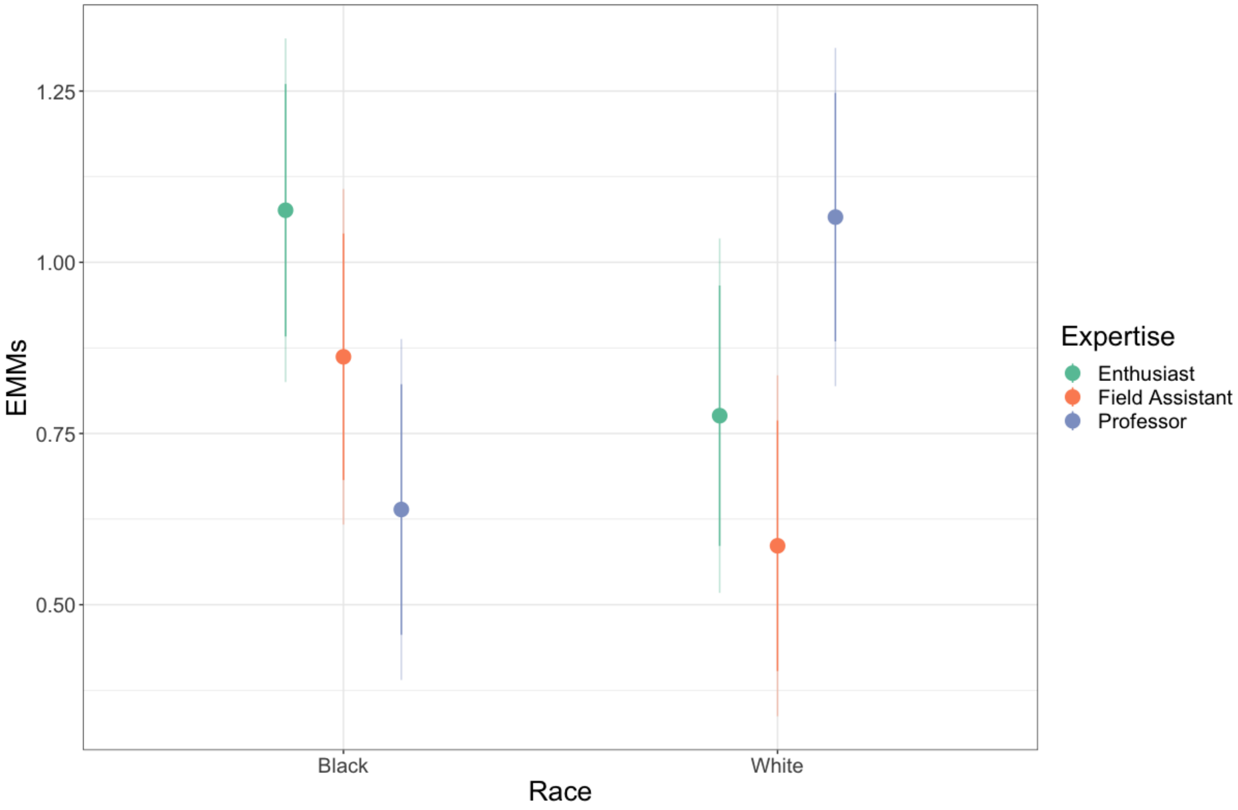


**Figure 4a. Associations between factor levels of the interaction term in the top-supported model for question 2.** Points show the estimated marginal means (EMMs) for the interaction between levels of race and expertise as present in the top-supported model for question 2- to what extent do you agree with Pat Rogers that we should relocate people to protect lions? Increasing EMMs indicate a more positive effect of that combination of factor levels on increasing levels of agreement. Coloured error bars show the 85% CIs, with transparent error bar extensions indicating the 95% CIs.

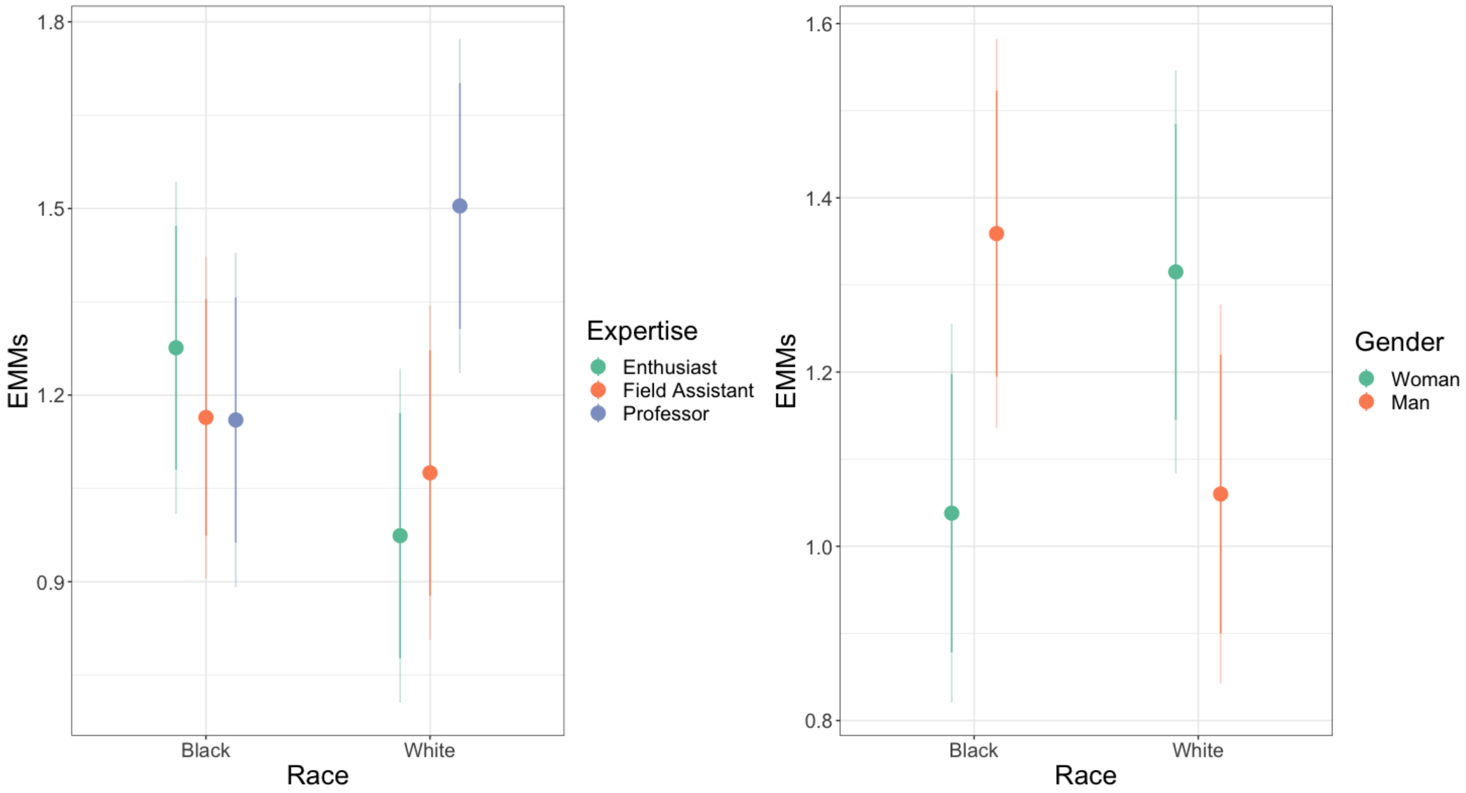


**Figure 4b and 4c. Associations between factor levels of the interaction terms in the top-supported model for question 3.** 4b shows the associations between levels of race and expertise, while 4c shows the association between levels of race and gender. Points show the estimated marginal means (EMMs) for the interactions present in the top-supported model for question 3- to what extent do you agree that Pat Rogers is a trustworthy source of lion conservation information? Increasing EMMs indicate a more positive effect of that combination of factor levels on increasing levels of agreement. Coloured error bars show the 85% CIs, with transparent error bar extensions indicating the 95% CIs.

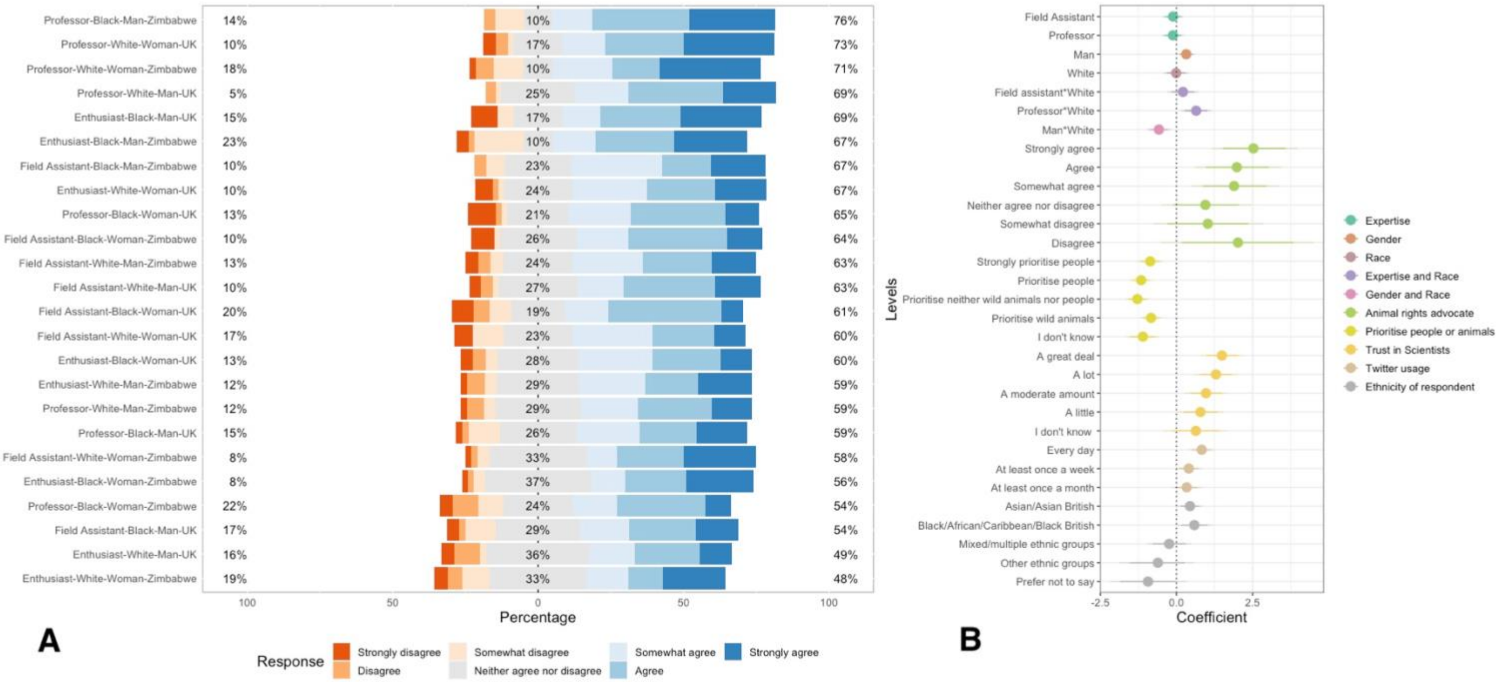


**Figure 5a. Agreement that Pat Rogers is a trustworthy source of lion conservation information, grouped by the experimental profile presented as expertise/race/gender/nationality.** Each bar represents the responses to one of the 24 profiles being tested, and shows the distribution of responses, coloured from reds (disagreement), through greys (neutrality) to blues (agreement). The percentage figures show the number of respondents who overall disagreed (left), were neutral (middle) or agreed (right), after excluding "I don't know" responses

**Figure 5b. Directional associations between agreement that Pat Rogers is a trustworthy source of lion conservation information, and the variables in the top-supported model.** Points indicate the log-odds ratios (or coefficient estimates) for the levels of each variable (shown in the key on the right hand side) relative to the reference category (expertise = enthusiast; gender = woman; race = Black; expertise and race = enthusiast*white; gender and race = woman*white; animal rights advocate = strongly disagree; prioritise people or animals = strongly prioritise wild animals; trust in scientists = no confidence; twitter usage = less than once a month; ethnicity = English/Welsh/Scottish/Northern Irish/British)**.** Positive coefficients demonstrate increased agreement comparative to the reference level, while negative coefficients demonstrate decreased agreement. Coloured error bars show the 85% CIs, with transparent error bar extensions indicating the 95% CIs.

## 4.7. References

*Citation Diversity Statement: Across scientific disciplines extensive bias in publication and citation practices have been identified, with those authored by marginalized scholars underrepresented* [87]. *As such, publication and citation practices continue to perpetuate inequities in academia. In writing this manuscript we have remained cognizant of such dynamics and striven to cite a diverse collective of authors.*

1. Ceballos, G., Ehrlich, P.R., and Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. *114*. https://doi.org/10.1073/pnas.1704949114.
2. Nielsen, K.S., Marteau, T.M., Bauer, J.M., Bradbury, R.B., Broad, S., Burgess, G., Burgman, M., Byerly, H., Clayton, S., Espelosin, D., et al. (2021). Biodiversity conservation as a promising frontier for behavioural science. Nat. Hum. Behav. *5*, 550–556. https://doi.org/10.1038/s41562-021-01109-5.
3. Duthie, E., Veríssimo, D., Keane, A., and Knight, A.T. (2017). The effectiveness of celebrities in conservation marketing. PLOS ONE *12*, e0180027. https://doi.org/10.1371/journal.pone.0180027.
4. Massingham, E.J., Wilson, K.A., Meijaard, E., Ancrenaz, M., Santika, T., Friedman, R., Possingham, H.P., and Dean, A.J. (2023). Public opinion on protecting iconic species depends on individual wellbeing: Perceptions about orangutan conservation in Indonesia and Malaysia. Environ. Sci. Policy *150*, 103588. https://doi.org/10.1016/j.envsci.2023.103588.
5. Wright, A.J., Veríssimo, D., Pilfold, K., Parsons, E.C.M., Ventre, K., Cousins, J., Jefferson, R., Koldewey, H., Llewellyn, F., and McKinley, E. (2015). Competitive outreach in the 21st century: Why we need conservation marketing. Ocean Coast. Manag. *115*, 41–48. https://doi.org/10.1016/j.ocecoaman.2015.06.029.
6. Crowley, S.L., Hinchliffe, S., and McDonald, R.A. (2017). Conflict in invasive species management. Front. Ecol. Environ. *15*, 133–141. https://doi.org/10.1002/fee.1471.
7. Macdonald, E.A., Burnham, D., Hinks, A.E., Dickman, A.J., Malhi, Y., and Macdonald, D.W. (2015). Conservation inequality and the charismatic cat: Felis felicis. Glob. Ecol. Conserv. *3*, 851–866. https://doi.org/10.1016/j.gecco.2015.04.006.

8. IUCN (2014). Panthera leo: Bauer, H., Packer, C., Funston, P.F., Henschel, P. & Nowell, K.: The IUCN Red List of Threatened Species 2016: e.T15951A115130419. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15951A107265605.en.

9. Bauer, H., Dickman, A., Chapron, G., Oriol-Cotterill, A., Nicholson, S.K., Sillero-Zubiri, C., Hunter, L., Lindsey, P., and Macdonald, D.W. (2022). Threat analysis for more effective lion conservation. Oryx *56*, 108–115. https://doi.org/10.1017/S0030605320000253.

10. Lindsey, P.A., Miller, J.R.B., Petracca, L.S., Coad, L., Dickman, A.J., Fitzgerald, K.H., Flyman, M.V., Funston, P.J., Henschel, P., Kasiki, S., et al. (2018). More than $1 billion needed annually to secure Africa's protected areas with lions. Proc. Natl. Acad. Sci. *115*. https://doi.org/10.1073/pnas.1805048115.

11. Kimaro, M.H., and Hughes, C. (2023). Conditions of Conflict: Exploring Pastoralist Resettlement in Relation to African Lion Conservation. Soc. Nat. Resour., 1–22. https://doi.org/10.1080/08941920.2023.2263861.

12. Macdonald, D.W., Jacobsen, K.S., Burnham, D., Johnson, P.J., and Loveridge, A.J. (2016). Cecil: A moment or a movement? Analysis of media coverage of the death of a lion, Panthera Leo. Animals *6*. https://doi.org/10.3390/ani6050026.

13. McCubbin, S.G. (2020). The Cecil Moment: Celebrity environmentalism, Nature 2.0, and the cultural politics of lion trophy hunting. Geoforum *108*, 194–203. https://doi.org/10.1016/j.geoforum.2019.10.015.

14. Chimuka, G. (2022). The role of the media and the international community in recent conservation issues in Sourthern Africa: The case of Cecil the lion. In Protected Areas and Tourism in Southern Africa (Routledge), pp. 146–160.

15. Hart, A.G., Cooney, R., Dickman, A., Hare, D., Jonga, C., Johnson, P.K., Louis, M.P., Lubilo, R., Roe, D., Semcer, C., et al. (2020). Threats posed to conservation by media misinformation. Conserv. Biol. *34*, 1333–1334. https://doi.org/10.1111/cobi.13605.

16. Macdonald, D.W., Johnson, P.J., Loveridge, A.J., Burnham, D., and Dickman, A.J. (2016). Conservation or the Moral High Ground: Siding with Bentham or Kant. Conserv. Lett. *9*, 307–308. https://doi.org/10.1111/conl.12254.

17. Nelson, M.P., Bruskotter, J.T., Vucetich, J.A., and Chapron, G. (2016). Emotions and the Ethics of Consequence in Conservation Decisions: Lessons from Cecil the Lion: Emotions and ethics in conservation decisions. Conserv. Lett. *9*, 302–306. https://doi.org/10.1111/conl.12232.

18. Van Eeden, L.M., Dickman, C.R., Ritchie, E.G., and Newsome, T.M. (2017). Shifting public values and what they mean for increasing democracy in wildlife management

decisions. Biodivers. Conserv. *26*, 2759–2763. https://doi.org/10.1007/s10531-017-1378-9.

19. Evans, L.C., Greenwell, M.P., Boult, V.L., and Johnson, T.F. (2023). Characterizing the trophy hunting debate on Twitter. Conserv. Biol. *37*, e14070. https://doi.org/10.1111/cobi.14070.

20. Yang, K.C., Pierri, F., Hui, P.M., Axelrod, D., Torres-Lugo, C., Bryden, J., and Menczer, F. (2021). The COVID-19 Infodemic: Twitter versus Facebook. Big Data Soc. *8*. https://doi.org/10.1177/20539517211013861.

21. Vosoughi, S., Roy, D., and Aral, S. (2018). The spread of true and false news online. Science *359*, 1146–1151. https://doi.org/10.1126/science.aap9559.

22. Lunstrum, E. (2017). Feed them to the lions: Conservation violence goes online. Geoforum *79*, 134–143. https://doi.org/10.1016/j.geoforum.2016.04.009.

23. Mkono, M. (2022). How we can make the trophy hunting debate less fraught. Nat. Hum. Behav. *7*, 6–8. https://doi.org/10.1038/s41562-022-01488-3.

24. Hare, D., Dickman, A.J., Johnson, P.J., Rono, B.J., Mutinhima, Y., Sutherland, C., Kulunge, S., Sibanda, L., Mandoloma, L., and Kimaili, D. (2024). Public perceptions of trophy hunting are pragmatic, not dogmatic. Proc. R. Soc. B Biol. Sci. *291*, 20231638. https://doi.org/10.1098/rspb.2023.1638.

25. Martín-López, B., Montes, C., Ramírez, L., and Benayas, J. (2009). What drives policy decision-making related to species conservation? Biol. Conserv. *142*, 1370–1380. https://doi.org/10.1016/j.biocon.2009.01.030.

26. Boling, K.S., and Walker, D. (2021). How Race and Gender Impact the Perceived Objectivity of Broadcast Women of Color on Twitter. Soc. Media Soc. *7*, 205630512110629. https://doi.org/10.1177/20563051211062921.

27. Groggel, A., Nilizadeh, S., Ahn, Y.Y., Kapadia, A., and Rojas, F. (2019). Race and the beauty premium: Mechanical Turk workers' evaluations of Twitter accounts. Inf. Commun. Soc. *22*, 709–716. https://doi.org/10.1080/1369118X.2018.1543443.

28. Kidd, L.R., Garrard, G.E., Bekessy, S.A., Mills, M., Camilleri, A.R., Fidler, F., Fielding, K.S., Gordon, A., Gregg, E.A., Kusmanoff, A.M., et al. (2019). Messaging matters: A systematic review of the conservation messaging literature. Biol. Conserv. *236*, 92–99. https://doi.org/10.1016/j.biocon.2019.05.020.

29. Mathiesen, K.E., Johansson, M., Barmoen, M., and Magnus, K. (2021). Trust in researchers and researchers ' statements in large carnivore conservation. 1–14. https://doi.org/10.1002/pan3.10282.

30. Sauer, K.A., Capps, D.K., Jackson, D.F., and Capps, K.A. (2021). Six minutes to promote change : People , not facts , alter students ' perceptions on climate change. 1–13. https://doi.org/10.1002/ece3.7553.

31. Hammond, N.L., Dickman, A., and Biggs, D. (2022). Examining attention given to threats to elephant conservation on social media. Conserv. Sci. Pract. *4*. https://doi.org/10.1111/csp2.12785.

32. Domínguez, L., and Luoma, C. (2020). Decolonising conservation policy: How colonial land and conservation ideologies persist and perpetuate indigenous injustices at the expense of the environment. Land *9*, 11–14. https://doi.org/10.3390/land9030065.

33. Kashwan, P., V. Duffy, R., Massé, F., Asiyanbi, A.P., and Marijnen, E. (2021). From Racialized Neocolonial Global Conservation to an Inclusive and Regenerative Conservation. Environ. Sci. Policy Sustain. Dev. *63*, 4–19. https://doi.org/10.1080/00139157.2021.1924574.

34. James, R., Fisher, J.R.B., Carlos-Grotjahn, C., Boylan, M.S., Dembereldash, B., Demissie, M.Z., Diaz De Villegas, C., Gibbs, B., Konia, R., Lyons, K., et al. (2023). Gender bias and inequity holds women back in their conservation careers. Front. Environ. Sci. *10*, 1056751. https://doi.org/10.3389/fenvs.2022.1056751.

35. Rudd, L.F., Allred, S., Bright Ross, J.G., Hare, D., Nkomo, M.N., Shanker, K., Allen, T., Biggs, D., Dickman, A., Dunaway, M., et al. (2021). Overcoming racism in the twin spheres of conservation science and practice. Proc. R. Soc. B Biol. Sci. *288*, 20211871. https://doi.org/10.1098/rspb.2021.1871.

36. Taylor, D.E. (2015). Gender and Racial Diversity in Environmental Organizations: Uneven Accomplishments and Cause for Concern. Environ. Justice *8*, 165–180. https://doi.org/10.1089/env.2015.0018.

37. Ashley-Smith, J. (2016). Losing the edge: the risk of a decline in practical conservation skills. J. Inst. Conserv. *39*.

38. Fernández-Llamazares, Á., Lepofsky, D., Lertzman, K., Armstrong, C.G., Brondizio, E.S., Gavin, M.C., Lyver, P.O., Nicholas, G.P., Pascua, P., Reo, N.J., et al. (2021). Scientists' Warning to Humanity on Threats to Indigenous and Local Knowledge Systems. J. Ethnobiol. *41*, 144–169. https://doi.org/10.2993/0278-0771-41.2.144.

39. Malmer, P., Vanessa, M., Austin, B., and Tengö, M. (2020). Mobilisation of indigenous and local knowledge as a source of useable evidence for conservation partnerships. In Conservation Research, Policy and Practice, W. J. Sutherland, P. N. M. Brotherton, Z. G. Davies, N. Ockendon, N. Pettorelli, and J. A. Vickery, eds. (Cambridge University Press), pp. 82–113. https://doi.org/10.1017/9781108638210.006.

40. Orlove, B., Sherpa, P., Dawson, N., Adelekan, I., Alangui, W., Carmona, R., Coen, D., Nelson, M.K., Reyes-García, V., Rubis, J., et al. (2023). Placing diverse knowledge systems at the core of transformative climate research. Ambio *52*, 1431–1447. https://doi.org/10.1007/s13280-023-01857-w.

41. Haelewaters, D., Hofmann, T.A., and Romero-Olivares, A.L. (2021). Ten simple rules for Global North researchers to stop perpetuating helicopter research in the Global South. PLOS Comput. Biol.

42. Miele, E. (2014). Using the Draw-a-Scientist Test for Inquiry and Evaluation. J. Coll. Sci. Teach. *43*, 36–40. https://doi.org/10.2505/4/jcst14_043_04_36.

43. Census - Office for National Statistics https://www.ons.gov.uk/census.

44. Strack, F. (1992). "Order Effects" in Survey Research: Activation and Information Functions of Preceding Questions. In Context Effects in Social and Psychological Research (Springer, New York, NY), pp. 23–34.

45. Bryer, J., and Speerschneider, K. (2016). Analysis and Visualization of Likert Items.

46. Christensen, R. (2023). Regression Models for Ordinal Data.

47. Barton´, K. (2023). Multi-Model Inference.

48. Arnold, T.W. (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J. Wildl. Manag. *74*, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x.

49. Leroux, S.J. (2019). On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. PLOS ONE *14*, e0206711. https://doi.org/10.1371/journal.pone.0206711.

50. Sutherland, C., Hare, D., Johnson, P.J., Linden, D.W., Montgomery, R.A., and Droge, E. (2023). Practical advice on variable selection and reporting using Akaike information criterion. Proc. R. Soc. B Biol. Sci. *290*, 20231261. https://doi.org/10.1098/rspb.2023.1261.

51. Lenth, R.V. (2024). Estimated Marginal Means, aka Least-Squares Means.

52. Wickham, H. (2024). Create Elegant Data Visualisations Using the Grammar of Graphics.

53. Giakoumi, S., Pita, C., Coll, M., Fraschetti, S., Gissi, E., Katara, I., Lloret-Lloret, E., Rossi, F., Portman, M., Stelzenmüller, V., et al. (2021). Persistent gender bias in marine science and conservation calls for action to achieve equity. Biol. Conserv. *257*, 109134. https://doi.org/10.1016/j.biocon.2021.109134.

54. James, R., Gibbs, B., Whitford, L., Leisher, C., Konia, R., and Butt, N. (2021). Conservation and natural resource management: where are all the women? Oryx *55*, 860–867. https://doi.org/10.1017/S0030605320001349.

55. Lau, J.D. (2020). Three lessons for gender equity in biodiversity conservation. Conserv. Biol. *34*, 1589–1591. https://doi.org/10.1111/cobi.13487.

56. Liévano-Latorre, L.F., Da Silva, R.A., Vieira, R.R.S., Resende, F.M., Ribeiro, B.R., Borges, F.J.A., Sales, L., and Loyola, R. (2020). Pervasive gender bias in editorial boards of biodiversity conservation journals. Biol. Conserv. *251*, 108767. https://doi.org/10.1016/j.biocon.2020.108767.

57. Zhu, J.M., Pelullo, A.P., Hassan, S., Siderowf, L., Merchant, R.M., and Werner, R.M. (2019). Gender Differences in Twitter Use and Influence Among Health Policy and Health Services Researchers. JAMA Intern. Med. *179*, 1726. https://doi.org/10.1001/jamainternmed.2019.4027.

58. Chapman, C., Hemingway, C., Sarkar, D., Gogarten, J., and Stenseth, NilsChr. (2022). Altmetric Scores in Conservation Science have Gender and Regional Biases. Conserv. Soc. *20*, 195. https://doi.org/10.4103/cs.cs_27_21.

59. Crenshaw, K. (1997). Demarginalizing the Intersection of Race and Sex. In Feminist Legal Theories (Routledge), p. 29.

60. Rosette, A.S., Ponce De Leon, R., Koval, C.Z., and Harrison, D.A. (2018). Intersectionality: Connecting experiences of gender with race at work. Res. Organ. Behav. *38*, 1–22. https://doi.org/10.1016/j.riob.2018.12.002.

61. Bumpus, N. (2020). Too many senior white academics still resist recognizing racism. Nature *583*, 661. https://doi.org/10.1038/d41586-020-02203-w.

62. Gewin, V. (2020). The time tax put on scientists of colour. Nature *583*, 479–481. https://doi.org/10.1038/d41586-020-01920-6.

63. Wright, C., Thompson, S., and Channer, Y. (2007). Out of Place: Black women academics in British universities. Womens Hist. Rev. *16*, 145–162. https://doi.org/10.1080/09612020601048704.

64. Lerchenmueller, M.J., Sorenson, O., and Jena, A.B. (2019). Gender differences in how scientists present the importance of their research: observational study. BMJ, l6573. https://doi.org/10.1136/bmj.l6573.

65. McKinnon, M., and O'Connell, C. (2020). Perceptions of stereotypes applied to women who publicly communicate their STEM work. Humanit. Soc. Sci. Commun. *7*, 160. https://doi.org/10.1057/s41599-020-00654-0.

66. UKRI diversity data for funding applicants and awardees 2020 to 21 update (2023). https://www.ukri.org/publications/diversity-data-for-funding-applicants-and-

awardees-2020-21/ukri-diversity-data-for-funding-applicants-and-awardees-2020-to-21-update/.

67. Abidin, C., Brockington, D., Goodman, M.K., Mostafanezhad, M., and Richey, L.A. (2020). The Tropes of Celebrity Environmentalism. Annu. Rev. Environ. Resour. *45*, 387–410. https://doi.org/10.1146/annurev-environ-012320-081703.

68. Brockington, D. (2009). Celebrity and the Environment: Fame, Wealth and Power in Conservation (Zed Books Ltd).

69. Frieze, C., and Marculescu, D. (2018). “Where Are You Really From?”: Mitigating Unconscious Bias on Campus.

70. Anderson, B., Böhmelt, T., and Ward, H. (2017). Public opinion and environmental policy output: a cross-national analysis of energy policies in Europe. Environ. Res. Lett. *12*, 114011. https://doi.org/10.1088/1748-9326/aa8f80.

71. Larson, L.R., Stedman, R.C., Cooper, C.B., and Decker, D.J. (2015). Understanding the multi-dimensional structure of pro-environmental behavior. J. Environ. Psychol. *43*, 112–124. https://doi.org/10.1016/j.jenvp.2015.06.004.

72. Chaudhury, A., and Colla, S. (2020). Next steps in dismantling discrimination: Lessons from ecology and conservation science. Conserv. Lett., e12774. https://doi.org/10.1111/conl.12774.

73. Taylor, D.E. (2014). The State of Diversity in Environmental Organizations. Green 20, 1–5. https://doi.org/10.13140/RG.2.2.32834.68804.

74. Bruskotter, J.T., Vucetich, J.A., Dietsch, A., Slagle, K.M., Brooks, J.S., and Nelson, M.P. (2019). Conservationists’ moral obligations toward wildlife: Values and identity promote conservation conflict. Biol. Conserv. *240*, 108296. https://doi.org/10.1016/j.biocon.2019.108296.

75. Lute, M.L., Bump, A., and Gore, M.L. (2014). Identity-Driven Differences in Stakeholder Concerns about Hunting Wolves. PLoS ONE *9*, e114460. https://doi.org/10.1371/journal.pone.0114460.

76. Schroeder, S.A., Landon, A.C., Fulton, D.C., and McInenly, L.E. (2021). Social identity, values, and trust in government: How stakeholder group, ideology, and wildlife value orientations relate to trust in a state agency for wildlife management. Biol. Conserv. *261*, 109285. https://doi.org/10.1016/j.biocon.2021.109285.

77. Van Eeden, L.M., Newsome, T.M., Crowther, M.S., Dickman, C.R., and Bruskotter, J. (2019). Social identity shapes support for management of wildlife and pests. Biol. Conserv. *231*, 167–173. https://doi.org/10.1016/j.biocon.2019.01.012.

78. Van Eeden, L.M., Slagle, K., Newsome, T.M., Crowther, M.S., Dickman, C.R., and Bruskotter, J.T. (2020). Exploring nationality and social identity to explain attitudes

toward conservation actions in the United States and Australia. Conserv. Biol. *34*, 1165–1175. https://doi.org/10.1111/cobi.13488.

79. Hendriks, F., Kienhues, D., and Bromme, R. (2016). Trust in Science and the Science of Trust. In Trust and Communication in a Digitized World (Springer), pp. 143–159.

80. McCright, A.M., Dentzman, K., Charters, M., and Dietz, T. (2013). The influence of political ideology on trust in science. Environ. Res. Lett. *8*, 044029. https://doi.org/10.1088/1748-9326/8/4/044029.

81. Turel, O., and Osatuyi, B. (2021). Biased Credibility and Sharing of Fake News on Social Media: Considering Peer Context and Self-Objectivity State. J. Manag. Inf. Syst. *38*, 931–958. https://doi.org/10.1080/07421222.2021.1990614.

82. Hiltzik: How Twitter lost its scientific mojo - Los Angeles Times https://www.latimes.com/business/story/2023-08-25/column-scientists-used-to-love-twitter-thanks-to-elon-musk-theyre-giving-up-on-it.

83. Cassidy, A. (2012). Vermin, Victims and Disease: UK Framings of Badgers In and Beyond the Bovine TB Controversy. Sociol. Rural. *52*, 192–214. https://doi.org/10.1111/j.1467-9523.2012.00562.x.

84. Chávez, K., and Mitchell, K.M.W. (2020). Exploring Bias in Student Evaluations: Gender, Race, and Ethnicity. PS Polit. Sci. Polit. *53*, 270–274. https://doi.org/10.1017/S1049096519001744.

85. MacNell, L., Driscoll, A., and Hunt, A.N. (2015). What’s in a Name: Exposing Gender Bias in Student Ratings of Teaching. Innov. High. Educ. *40*, 291–303. https://doi.org/10.1007/s10755-014-9313-4.

86. Hofstra, B., Kulkarni, V.V., Galvez, S.M.N., He, B., Jurafsky, D., and McFarland, D.A. (2020). The diversity–innovation paradox in science. Proc. Natl. Acad. Sci. U. S. A. *117*, 9284–9291. https://doi.org/10.1073/pnas.1915378117.

87. Zurn, P., Bassett, D.S., and Rust, N.C. (2020). The Citation Diversity Statement: A Practice of Transparency, A Way of Life. Trends Cogn. Sci. *24*, 669–672. https://doi.org/10.1016/j.tics.2020.06.009.

# 4.8. Supplementary information

## Appendix S1. Full Questionnaire

### SECTION 1- LANDING PAGE

Please read through the information below about our study before deciding whether to participate. You may ask any questions before deciding to take part by contacting the principal researcher (details below).

By participating in this online survey about the credibility of lion conservation recommendations (it will take approximately 5-10 minutes), you will help us understand how people respond to information about lion conservation on Twitter. You do not need any specialist background knowledge to participate. Our results from this study might help to inform how conservationists frame messages about lion conservation.

We will store the responses you provide in a password-protected electronic file. We will not ask you to provide any information that would identify you and we will not store your IP address. Only researchers working directly on this study will have access to the information you provide.

The data you provide may be transferred to, stored and/or processed at a destination outside the UK and the European Economic Area ("EEA"). By submitting data, you agree to this transfer, storing or processing. We may use the information you provide in academic publications such as reports and journal articles, but we will only analyze and report responses in general terms.

Qualtrics LLC is the data controller with respect to your personal data and, as such, will determine how your personal data is used. Please see their privacy notice here [www.qualtrics.com/privacy-statement/]. Qualtrics LLC will share only de-identified data with the University of Oxford, for the purposes of research.

If you choose to participate, we will first ask some questions to determine whether you are eligible for the study.

You can choose to withdraw for any reason at any point during the study by closing your browser tab. You will receive payment for participation if you complete the study, which includes answering some required questions. Some parts of the questionnaire mention people and/or animals dying, but there are no pictures or graphic descriptions.

This project has been reviewed by, and received ethics clearance through, a subcommittee of the University of Oxford Central University Research Ethics Committee [reference number R79948/RE001].

The principal researcher is Lauren Rudd, who works in the Wildlife Conservation Research Unit in the Zoology Department at the University of Oxford. This study is being conducted in collaboration with other researchers at the University of Oxford and Cornell University.

If you have a concern about any aspect of this study, please email Lauren Rudd (lauren.rudd@gtc.ox.ac.uk) and we will do our best to answer your query. We will acknowledge your concern within 10 working days and give you an indication of how we will deal with it. If you remain unhappy or wish to make a formal complaint, please contact the Chair of the Medical Sciences Interdivisional Research Ethics Committee at the University of Oxford who will seek to resolve the matter as soon as possible: Email: ethics@medsci.ox.ac.uk; Address: Research Services, University of Oxford, Boundary Brook House, Churchill Drive, OX3 7GB.

By confirming you are 18 or older and selecting "Yes, I agree to take part" below, you indicate that you voluntarily agree to participate in this study.

Please note that you may only participate in this study only if you are 18 years of age or over.

☐ I certify that I am 18 years of age or over

If you have read the information above and agree to participate with the understanding that the data you submit will be processed accordingly, please check the relevant box below to get started.

☐ Yes, I agree to take part

*After providing consent, respondents will answer a few general questions to confirm eligibility and prevent oversampling from some demographics. This means we collect data only from eligible respondents, so we will not waste ineligible respondents' time.*

| *Item number* | *Measuring* | *Item* | *Response options* |
|---|---|---|---|
| 1.1 | Gender Quota | Which best describes how you identify your gender? | · Woman<br>· Man<br>· Non-binary<br>· In another way<br>· Prefer not to say |
| 1.2 | Age quota | How old are you? | · 18-29<br>· 30-44<br>· 45-59<br>· 60 or older<br>· Prefer not to say |

| | | | |
|---|---|---|---|
| 1.3 | Ethnicity Quota | Which best describes how you identify your ethnicity? | White<br>· English/Welsh/Scottish/Northern Irish/British<br>· Irish<br>· Gypsy or Irish Traveler<br>· Any other White background<br>Asian/Asian British<br>· Indian<br>· Pakistani<br>· Bangladeshi<br>· Chinese<br>· Any other Asian background<br>Black/African/Caribbean/Black British<br>· African<br>· Caribbean<br>· Any other Black/African/Caribbean background<br>Mixed/Multiple ethnic groups<br>· White and Black Caribbean<br>· White and Black African<br>· White and Asian<br>· Any other Mixed/Multiple ethnic background<br>Other ethnic group<br>· Arab<br>· Any other ethnic group<br>· Prefer not to say |
| 1.4 | Twitter usage | Approximately how often have you used Twitter in the past 6 months? *This could involve posting your own content and/or reading content posted by others* | · Every day<br>· About once a week<br>· About once a month<br>· Less than once a month |

## SECTION 2: BACKGROUND/CONTEXT PAGE

Please carefully read the information below, which describes the current situation surrounding lion conservation and management.

It is estimated that there are as few as 23,000 wild lions living in Africa today, around half as many as there were 20 years ago. Many lions live in protected areas such as national parks. As lions require large areas, they often move into land surrounding protected areas, where people live.

More than a quarter of the area where lions still exist is entirely outside of protected areas, alongside people. Many of the people that live alongside lions keep livestock such as goats and cows, which are essential to their livelihoods.

Some of the biggest threats to lions today are the loss of wild habitat and prey, and human-lion conflict, for example, when people legally or illegally kill lions to protect themselves or their livestock.

Moving “problem lions” that prey on livestock to a different place can sometimes reduce human-lion conflict in the original area. However, doing so can also increase human-lion conflict in the area where the lions are relocated, with risks for both people (who might suffer attacks) and lions (who might then be killed).

Lion conservation is expensive, and in most places, photo-tourism alone cannot cover the costs of effective conservation. Legal, regulated trophy hunting of lions can generate additional funding to incentivise conservation and may create local income and jobs.

Some people believe that trophy hunting lions is acceptable. However, others believe that killing lions, especially for recreation or trophies, is unacceptable.

When you have read this information, please click “Next”.

## SECTION 3: MAIN STUDY- CREDIBILITY OF CONSERVATION INFORMATION ON TWITTER

*Each respondent was presented with one fictitious Twitter (now X) profile image as shown below, alongside the following questions.*

**Pat Rogers** 🦁
@PatRogers10

Lion Conservation enthusiast, United Kingdom.❤️ Big Cats! Views my own.
RTs not endorsement. She/her 🇬🇧

United Kindgom Joined June 2015

**468** Following **2,693** Followers

**Pat Rogers** 🦁 @PatRogers10 · 18 Jan 2021
If people are living in conflict with lions, those people must be relocated to protect lions and their habitats. We must keep lions safe from people at all costs. 👍🏾

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On this page you will see the Twitter profile of Pat Rodgers, who works in lion conservation, and you will be asked questions about the information their profile contains.

Your responses will help us understand how people respond to information about lion conservation on Twitter.

Please indicate how strongly you agree or disagree with each statement. If you are indifferent, please select "neither agree nor disagree". If you do not know whether you agree or disagree, please select "I don't know".

| *Item number* | *Question* | *Response options* |
|---|---|---|
| 3.1 | To what extent do you agree that the information presented in Pat Rodgers’ pinned tweet is credible? | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 3.2 | To what extent do you agree with Pat Rodgers that we should relocate people to address human-lion conflict? | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |

| | | |
|---|---|---|
| 3.3 | To what extent do you agree that Pat Rodgers is a trustworthy source of lion conservation information? | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |

## SECTION 4: DEMOGRAPHICS AND SOCIAL IDENTITY

On this page you will answer some general questions about your background and identity. You answered some of these questions before entering the study, and we are asking you to answer them again now as part of the study.

By answering these questions as accurately as you can, you will help us understand how people from different backgrounds and identities interact with information about lion conservation on Twitter. All information you provide is confidential.

| *Item number* | *Measuring* | *Item* | *Response options* |
|---|---|---|---|
| 4.1 | Age | What is your age in years? | · Whole numbers between 18 and 110 only |
| 4.2 | Formal education | What is the highest level of formal education you have completed? | · Primary school<br>· Secondary School<br>· College or university degree<br>· Postgraduate degree |
| 4.3 | Social identity: social justice | I think of myself as someone who supports equal access, rights, and opportunities for everyone. Do you… | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |

| | | | |
|---|---|---|---|
| 4.4 | Social identity: human rights | I think of myself as someone who supports human rights. Do you… | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 4.5 | Social identity: animal rights | I think of myself as someone who supports animal rights. Do you… | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 4.6 | People versus animals orientation | If the interests of wild animals clash with the interests of people, which do you think should be prioritized? | · Strongly prioritize wild animals<br>· Prioritize wild animals<br>· Prioritize neither wild animals nor people<br>· Prioritize people<br>· Strongly prioritize people<br>· I don’t know |

|  |  |  |  |
|---|---|---|---|
| 4.7 | Trust in expertise | How much confidence do you have in each of the following to advise, make decisions and act in the best interest of the public?<br>a) research scientists<br>b) elected officials/government agency workers<br>c) NGO/private sector workers | · No confidence<br>· Very little confidence<br>· Some confidence<br>· A lot of confidence<br>· Full confidence<br>· I don't know |

## SECTION 5: LEAVING PAGE

Thank you very much for participating in this study. Please click "submit" to record your responses.

This project has been reviewed by, and received ethics clearance through, the University of Oxford Central University Research Ethics Committee [reference number R79948/RE001].

The principal researcher is Lauren Rudd, who works in the Wildlife Conservation Research Unit in the Zoology Department at the University of Oxford.

If you have a concern about any aspect of this study, please email Lauren Rudd (lauren.rudd@gtc.ox.ac.uk), and we will do our best to answer your query. We will acknowledge your concern within 10 working days and give you an indication of how we will deal with it. If you remain unhappy or wish to make a formal complaint, please contact the Chair of the Medical Sciences Interdivisional Research Ethics Committee at the University of Oxford who will seek to resolve the matter as soon as possible: Email: ethics@medsci.ox.ac.uk.

## Appendix S2. Participant statistics

Descriptive statistics of participants in the final data set for the main study (n= 1290), broken down by demographic characteristics and social identities.

| **Characteristic** | **Responses** | **Count (%)** |
|---|---|---|
| | | |
| Gender Identity | Woman | 659 (51.1) |
| | Man | 625 (48.4) |
| | Non-binary | 5 (0.4) |
| | Prefer not to say | 1 (0.1) |
| | | |
| Age Group | 18-29 | 244 (18.9) |
| | 30-44 | 324 (25.1) |
| | 45-59 | 322 (25.0) |
| | 60+ | 400 (31.0) |
| | | |
| Ethnicity of respondent | White | 1110 (86.0) |
| | *English/Welsh/Scottish/Northern Irish/British* | *730 (56.6)* |
| | *Irish* | *69 (5.3)* |
| | *Gypsy or Irish Traveller* | *5 (0.4)* |
| | *Any other White background* | *306 (23.7)* |
| | Asian/Asian British | 86 (6.6) |
| | *Indian* | *25 (1.9)* |

| | | |
|---|---|---|
| | *Pakistani* | *4 (0.3)* |
| | *Bangladeshi* | *0 (0)* |
| | *Chinese* | *22 (1.7)* |
| | *Any other Asian/Asian British background* | *35 2.7)* |
| | Black/African/Caribbean/Black British | 44 (3.4) |
| | *African* | *28 ( 2.2)* |
| | *Caribbean* | *4 (0.3)* |
| | *Any other Black/African/Caribbean background* | *12 (0.9)* |
| | Mixed/multiple ethnic groups | 31 (2.3) |
| | *White and Black Caribbean* | *4 (0.3)* |
| | *White and Black African* | *7 (0.5)* |
| | *White and Asian* | *7 (0.5)* |
| | *Any other Mixed/Multiple ethnic groups background* | *13 (1.0)* |
| | Other ethnic groups | 10 (0.8) |
| | *Arab* | *1 (0.1)* |
| | *Any other ethnic group* | *9 (0.7)* |
| | Prefer not to say | 9 (0.7) |
| | | |
| Twitter usage | Less than once a month | 89 (6.9) |
| | At least once a month | 153 (11.9) |
| | At least once a week | 498 (38.6) |
| | Every day | 550 (42.6) |
| | | |

| | | |
|---|---|---|
| Highest level of formal education | Primary school | 39 (3.0) |
| | Secondary school | 413 (32.0) |
| | College or University undergraduate degree | 647 (50.2) |
| | Postgraduate degree | 174 (13.5) |
| | Prefer not to say | 17 ( 1.3) |
| | | |
| | | |
| Self reported social identity: support for human rights | Strongly disagree | 10 ( 0.8) |
| | Disagree | 4 ( 0.3) |
| | Somewhat disagree | 3 ( 0.2) |
| | Neither agree nor disagree | 41 ( 3.2) |
| | Somewhat agree | 122 ( 9.5) |
| | Agree | 406 (31.5) |
| | Strongly agree | 703 (54.5) |
| | I don't know | 1 ( 0.1) |
| | | |
| Self reported social identity: support for animal rights | Strongly disagree | 10 ( 0.8) |
| | Disagree | 3 ( 0.2) |
| | Somewhat disagree | 9 ( 0.7) |
| | Neither agree nor disagree | 61 ( 4.7) |
| | Somewhat agree | 153 (11.9) |
| | Agree | 387 (30.0) |
| | Strongly agree | 665 (51.6) |

| | | |
|---|---|---|
| | I don't know | 2 ( 0.2) |
| | | |
| Prioritise people or wild animals | Strongly prioritize wild animals | 174 (13.5) |
| | Prioritize wild animals | 332 (25.7) |
| | Prioritize neither wild animals nor people | 260 (20.2) |
| | Prioritize people | 276 (21.4) |
| | Strongly prioritize people | 163 (12.6) |
| | I don't know | 85 ( 6.6) |
| | | |
| Confidence in research scientists to act in public interest | None at all | 41 ( 3.2) |
| | A little | 122 ( 9.5) |
| | A moderate amount | 333 (25.8) |
| | A lot | 331 (25.7) |
| | A great deal | 440 (34.1) |
| | I don't know | 23 ( 1.8) |

## Appendix S3. Message selection preliminary study

To determine which lion conservation message to use in the pinned post we first conducted a preliminary message-selection study.

### Methods

We tested the response to four possible messages, each of which reflected tangible strategies to address existing lion conservation problems (see Appendix S3.1). The aim was to select a message that generated responses with a neutral central tendency and that was not obviously polarizing (i.e. with a mean value away from either extreme and with low variance). This would allow us to best interpret any effect of bias in the main study.

All authors were involved in the process of generating these proposed messages and designing the preliminary questionnaire (Appendix S3.2). Our study received ethics clearance through the University of Oxford Central University Research Ethics Committee (reference R79948/RE001).

We ran the study on the Qualtrics platform between 31 May and 7 June 2022. A total of 500 participants were recruited using Prolific. Participants were aged 18 or over and lived in the UK. All provided informed consent before starting the questionnaire and received compensation for taking part. All respondents that completed the survey in less than half the median duration time were removed from the final analysis (see Appendix S3.3).

Respondents were first presented with a short block of text about lion conservation and management strategies, to ensure they understood the topic sufficiently to answer the questionnaire, irrespective of their own prior knowledge (included with the full questionnaire in Appendix S1). Each participant was randomly presented with one of the four messages in Appendix S3.1 and was asked the extent to which they agreed with the lion conservation recommendation, using a seven-point bipolar Likert-type scale to record responses, from strongly disagree to strongly agree, with an additional “I don’t know” option. Prior to analysis, we converted responses to a numeric scale (strongly disagree = 1, strongly agree = 7) and removed “I don’t know” responses. Respondents also answered several demographic questions (gender, age, ethnicity, and level of formal education) as well as a block of questions about their social identities (extent of support for animal rights, human rights, and trust in scientists to act in the best interest of the public).

After the omission of those who completed the survey in less than half the median time, (163.5 seconds) to remove potentially unreliable responses from those who did not properly engage with the questions, the total number of respondents across the survey was n= 469. We analyzed data using the “likert” package in R (and calculated the mean and standard deviation for each message. These variables were compared across messages, and that with the fewest “I don’t know” responses, normally distributed data with low standard deviation, and with a mean response closest to 3 or 5 (somewhat agree or somewhat disagree) was chosen for use in the main study. We chose not to use a message which garnered a neutral response (mean close to 4) as this could be indicative of a topic that does not generate any opinion and so would not be influenced by identity bias.

### Message selection results

The acceptability of the messages about different lion conservation strategies varied considerably (Appendix S3.4). Both messages about trophy hunting generated highly skewed data with 88% of people strongly agreeing, agreeing, or somewhat agreeing that we should prevent trophy hunting (M = 5.983, SD = 1.119), and 83% of people strongly disagreeing, disagreeing, or somewhat disagreeing that we should permit trophy hunting (M= 2.244, SD= 1.562) (Appendix S3.5). As such, these messages were excluded from consideration for use in the main study.

The “Relocate lions” message generated slightly skewed data around the neutral “neither agree nor disagree” option; with 61% of people strongly agreeing, agreeing, or somewhat agreeing, while 28% strongly disagreed, disagreed, or somewhat disagreed (M= 4.593, SD= 1.492) (Appendix S3.5).

The “Relocate people” message generated normally distributed data around the “somewhat agree” option; with 64% strongly agreeing, agreeing, or somewhat agreeing, while 19% strongly disagreed, disagreed, or somewhat disagreed (M = 4.917, SD = 1.498) (Appendix S3.5).

We therefore selected the “Relocate people” message for use in the main study.

## Appendix S3.1. Candidate messages

The four candidate lion conservation messages that were tested, with participants randomly assigned one message and asked the extent to which they agreed with the statement using a 7-point Likert scale.

| | |
|---|---|
| Message 1 | We need to protect lions and keep them safe from people. Preventing trophy hunting will help achieve this, even if some people lose their livelihoods. |
| Message 2 | We need to protect people and their livelihoods and keep them safe from lions. Permitting trophy hunting will help achieve this, even if some lions lose their lives. |
| Message 3 | If people are living in conflict with lions, those people must be relocated to protect lions and their habitats. We must keep lions safe from people at all costs. |
| Message 4 | If lions are living in conflict with lions, those lions must be relocated to protect people’s safety and livelihoods. We must keep people safe from lions at all costs. |

# Appendix S3.2. Full message selection study questionnaire

## SECTION 1: LANDING PAGE

Please read through the information below about our study before deciding whether to participate. You may ask any questions before deciding to take part by contacting the principal researcher (details below).

By participating in this online survey about lion conservation recommendations (it will take approximately 5-10 minutes), you will help us understand how people respond to information about lion conservation. You do not need any specialist background knowledge to participate. Our results from this study might help to inform how conservationists frame messages about lion conservation.

We will store the responses you provide in a password-protected electronic file. We will not ask you to provide any information that would identify you and we will not store your IP address. Only researchers working directly on this study will have access to the information you provide.

The data you provide may be transferred to, stored and/or processed at a destination outside the UK and the European Economic Area ("EEA"). By submitting data, you agree to this transfer, storing or processing. We may use the information you provide in academic publications such as reports and journal articles, but we will only analyze and report responses in general terms.

Qualtrics LLC is the data controller with respect to your personal data and, as such, will determine how your personal data is used. Please see their privacy notice here [www.qualtrics.com/privacy-statement/]. Qualtrics LLC will share only de-identified data with the University of Oxford, for the purposes of research.

If you choose to participate, we will first ask some questions to determine whether you are eligible for the study.

You can choose to withdraw for any reason at any point during the study by closing your browser tab. You will receive payment for participation if you complete the study, which includes answering some required questions. Some parts of the questionnaire mention people and/or animals dying, but there are no pictures or graphic descriptions.

This project has been reviewed by, and received ethics clearance through, a subcommittee of the University of Oxford Central University Research Ethics Committee [reference number R79948/RE001].

The principal researcher is Lauren Rudd, who works in the Wildlife Conservation Research Unit in the Zoology Department at the University of Oxford. This study is being conducted in collaboration with other researchers at the University of Oxford and Cornell University.

If you have a concern about any aspect of this study, please email Lauren Rudd (lauren.rudd@gtc.ox.ac.uk) and we will do our best to answer your query. We will acknowledge your concern within 10 working days and give you an indication of how we will deal with it. If you remain unhappy or wish to make a formal complaint, please contact the Chair of the Medical Sciences Interdivisional Research Ethics Committee at the University of Oxford who will seek to resolve the matter as soon as possible: Email: ethics@medsci.ox.ac.uk; Address: Research Services, University of Oxford, Boundary Brook House, Churchill Drive, OX3 7GB.

By confirming you are 18 or older and selecting "Yes, I agree to take part" below, you indicate that you voluntarily agree to participate in this study.

**Please note that you may only participate in this study only if you are 18 years of age or over.**

☐ I certify that I am 18 years of age or over

**If you have read the information above and agree to participate with the understanding that the data you submit will be processed accordingly, please check the relevant box below to get started.**

☐ Yes, I agree to take part

## SECTION 2: BACKGROUND/CONTEXT PAGE

Please carefully read the information below, which describes the current situation surrounding lion conservation and management.

It is estimated that there are as few as 23,000 wild lions living in Africa today, around half as many as there were 20 years ago. Many lions live in protected areas such as national parks. As lions require large areas, they often move into land surrounding protected areas, where people live.

More than a quarter of the area where lions still exist is entirely outside of protected areas, alongside people. Many of the people that live alongside lions keep livestock such as goats and cows, which are essential to their livelihoods.

Some of the biggest threats to lions today are the loss of wild habitat and prey, and human-lion conflict, for example, when people legally or illegally kill lions to protect themselves or their livestock.

Moving “problem lions” that prey on livestock to a different place can sometimes reduce human-lion conflict in the original area. However, doing so can also increase human-lion conflict in the area where the lions are relocated, with risks for both people (who might suffer attacks) and lions (who might then be killed).

Lion conservation is expensive, and in most places, photo-tourism alone cannot cover the costs of effective conservation. Legal, regulated trophy hunting of lions can generate additional funding to incentivize conservation and may create local income and jobs.

Some people believe that trophy hunting lions is acceptable. However, others believe that killing lions, especially for recreation or trophies, is unacceptable.

When you have read this information, please click “Next”.

## SECTION 3: MESSAGE SELECTION

*Each respondent was presented with the instructions below, and only one of the "item numbers" from 3.1 to 3.4.*

On this page you will read a short statement about lion conservation.

Please indicate the extent to which you agree with the conservation recommendation highlighted in the statement. If you are indifferent, please select "neither support nor oppose". If you do not know whether you support it or oppose it, please select "I don't know".

| *Item number* | *Message* | *Response options* |
|---|---|---|
| 3.1 | We need to protect lions and keep them safe from people. Preventing trophy hunting will help achieve this, even if some people lose their livelihoods. | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don't know |

|  |  |  |
|---|---|---|
| 3.2 | We need to protect people and their livelihoods and keep them safe from lions. Permitting trophy hunting will help achieve this, even if some lions lose their lives. | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 3.3 | If people are living in conflict with lions, those people must be relocated to protect lions and their habitats. We must keep lions safe from people at all costs. | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 3.4 | If people are living in conflict with lions, those lions must be relocated to protect people’s safety and livelihoods. We must keep people safe from lions at all costs. | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |

## SECTION 4: DEMOGRAPHICS AND SOCIAL IDENTITY

On this page you will answer some general questions about your background and identity.

By answering these questions as accurately as you can, you will help us understand how people from different backgrounds and identities interact with information about lion conservation. All information you provide is confidential.

| *Item number* | *Measuring* | *Item* | *Response options* |
|---|---|---|---|
| 4.1 | Gender | Which best describes how you identify your gender? | · Woman<br>· Man<br>· Non-binary<br>· In another way<br>· Prefer not to say<br>· |
| 4.2 | Age | How old are you? | · 18-29<br>· 30-44<br>· 45-59<br>· 60 or older<br>· Prefer not to say<br>· |

| | | | |
|---|---|---|---|
| 4.3 | Ethnicity | Which best describes how you identify your ethnicity? | White<br>· English/Welsh/Scottish/Northern Irish/British<br>· Irish<br>· Gypsy or Irish Traveler<br>· Any other White background<br>Asian/Asian British<br>· Indian<br>· Pakistani<br>· Bangladeshi<br>· Chinese<br>· Any other Asian background<br>Black/African/Caribbean/Black British<br>· African<br>· Caribbean<br>· Any other Black/African/Caribbean background<br>Mixed/Multiple ethnic groups<br>· White and Black Caribbean<br>· White and Black African<br>· White and Asian<br>· Any other Mixed/Multiple ethnic background<br>Other ethnic group<br>· Arab<br>· Any other ethnic group<br>· Prefer not to say |
| 4.4 | Formal education | What is the highest level of formal education you have completed? | · Primary school<br>· Secondary School<br>· College or university degree<br>· Postgraduate degree |

|  |  |  |  |
|---|---|---|---|
| 4.5 | Social identity: social justice | I think of myself as someone who supports equal access, rights, and opportunities for everyone. Do you… | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 4.6 | Social identity: human rights | I think of myself as someone who supports human rights. Do you… | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |
| 4.7 | Social identity: animal rights | I think of myself as someone who supports animal rights. Do you… | · Strongly disagree<br>· Disagree<br>· Somewhat disagree<br>· Neither agree nor disagree<br>· Somewhat agree<br>· Agree<br>· Strongly agree<br>· I don’t know |

| | | | |
|---|---|---|---|
| 4.8 | Trust in expertise | How much confidence do you have in each of the following to advise, make decisions and act in the best interest of the public?<br>a) research scientists<br>b) elected officials/government agency workers<br>c) NGO/private sector workers | · No confidence<br>· Very little confidence<br>· Some confidence<br>· A lot of confidence<br>· Full confidence<br>· I don't know |

## SECTION 5: LEAVING PAGE

Thank you very much for participating in this study. Please click "submit" to record your responses.

This project has been reviewed by, and received ethics clearance through, the University of Oxford Central University Research Ethics Committee [reference number R79948/RE00].

The principal researcher is Lauren Rudd, who works in the Wildlife Conservation Research Unit in the Zoology Department at the University of Oxford.

If you have a concern about any aspect of this study, please email Lauren Rudd (lauren.rudd@gtc.ox.ac.uk), and we will do our best to answer your query. We will acknowledge your concern within 10 working days and give you an indication of how we will deal with it. If you remain unhappy or wish to make a formal complaint, please contact the Chair of the Medical Sciences Interdivisional Research Ethics Committee at the University of Oxford who will seek to resolve the matter as soon as possible: Email: ethics@medsci.ox.ac.uk.

## Appendix S3.3. Preliminary study participant descriptive statistics

Descriptive statistics of participants in the preliminary study data set (n= 469), broken down by demographic characteristics and social identities.

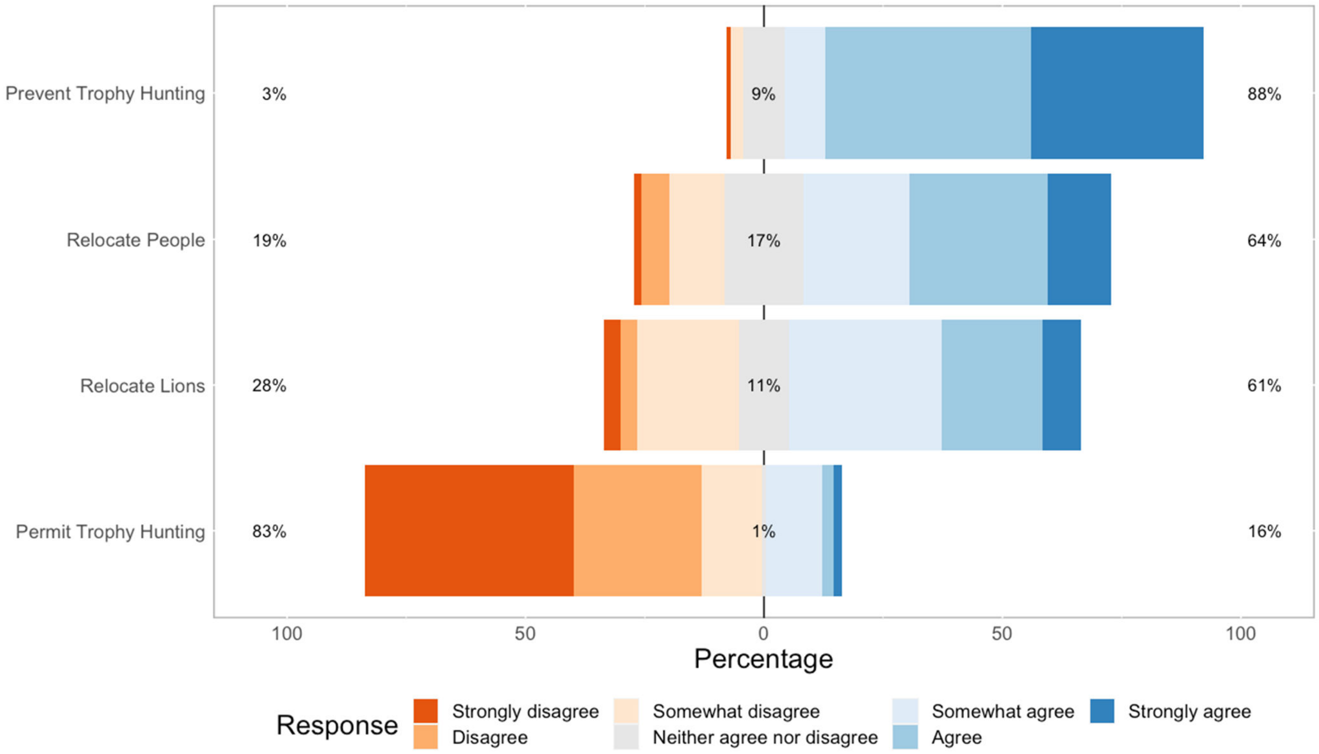
| **Characteristic** | **Responses** | **Count (%)** |
|---|---|---|
| Gender Identity | Woman | 227 (48.4) |
| | Man | 238 (50.7) |
| | Non-binary | 3 (0.6) |
| | In another way | 1 (0.2) |
| | | |
| Ethnicity (%) | White | 418 (89.1) |
| | *English/Welsh/Scottish/Northern Irish/British* | *372 (79.3)* |
| | *Irish* | *2 (0.4)* |
| | *Any other White background* | *44 (9.4)* |
| | Asian/Asian British | 23 (4.9) |
| | *Indian* | *6 (1.3)* |
| | *Pakistani* | *3 (0.6)* |
| | *Bangladeshi* | *1 (0.2)* |
| | *Chinese* | *5 (1.1)* |
| | *Any other Asian/Asian British background* | *8 (1.7)* |
| | Black/African/Caribbean/Black British | 12 (2.6) |
| | *African* | *8 (1.7)* |
| | *Caribbean* | *4 (0.9)* |
| | Mixed/multiple ethnic groups | 15 (3.3) |
| | *White and Black Caribbean* | *4 (0.9)* |
| | *White and Black African* | *4 (0.9)* |
| | *White and Asian* | *4 (0.9)* |
| | *Any other Mixed/Multiple ethnic groups background* | *3 (0.6)* |

| | | |
|---|---|---|
| | Prefer not to say | 2 (0.4) |
| | | |
| Age Group | 18-29 | 136 (29.0) |
| | 30-44 | 201 (42.9) |
| | 45-59 | 91 (19.4) |
| | 60+ | 41 (8.7) |
| | | |
| Highest level of formal education | Primary school | 2 (0.4) |
| | Secondary school | 104 (22.2) |
| | College or University undergraduate degree | 255 (54.4) |
| | Postgraduate degree | 106 (22.6) |
| | Prefer not to say | 2 (0.4) |
| | | |
| Self-reported social identity: support for human rights | Strongly disagree | 2 (0.4) |
| | Neither agree nor disagree | 12 (2.6) |
| | Somewhat agree | 44 (9.4) |
| | Agree | 171 (36.5) |
| | Strongly agree | 240 (51.2) |
| | | |
| Self-reported social identity: support for animal rights | Strongly disagree | 1 (0.2) |
| | Disagree | 3 (0.6) |
| | Somewhat disagree | 5 (1.1) |
| | Neither agree nor disagree | 22 (4.7) |
| | Somewhat agree | 70 (14.9) |
| | Agree | 166 (35.4) |
| | Strongly agree | 202 (43.1) |
| | | |
| Confidence in research scientists to act in public interest | None at all | 11 ( 2.3) |

| | | |
|---|---|---|
| | A little | 23 ( 4.9) |
| | A moderate amount | 98 (20.3) |
| | A lot | 131 (27.9) |
| | A great deal | 202 (43.1) |
| | I don't know | 7 (1.5) |

## Appendix S3.4. Agreement with each of the tested lion conservation messages.

Likert plot showing responses to all four candidate messages. Bars represent one message each and show the distribution of responses, coloured from reds (disagreement), through grays (neutrality), to blues (agreement). The percentage figures show the number of participants who overall disagreed (left), were neutral (middle), or agreed (right) after removing “I don’t know” responses.



## Appendix S3.5. Message selection results

Results of the message selection study showing the mean response (ranging from 1= strongly disagree to 7= strongly agree), standard deviation, and number of respondents for each of the four options tested.

| | Mean | SD | N |
|---|---|---|---|
| Prevent Trophy Hunting | 5.983 | 1.119 | 116 |
| Permit Trophy Hunting | 2.244 | 1.562 | 119 |
| Relocate People | 4.917 | 1.498 | 121 |
| Relocate Lions | 4.593 | 1.492 | 113 |

## Appendix S4.1. AIC weights table for question 1

Results of model selection process for question 1 after removing redundant and uninformative parameters, showing the top-supported model and all models within Δ2 $AIC_c$.

| **Model** | **df** | **logLik** | **$AIC_c$** | **delta** | **$AIC_w$** |
|---|---|---|---|---|---|
| age + animal rights + respondent ethnicity + character gender + human rights + people vs animals + trust in scientists + twitter usage | 38 | -2032.706 | 4143.854 | 0 | 0.217 |
| age + animal rights + respondent ethnicity + human rights + people vs animals + trust in scientists + twitter usage | 37 | -2033.867 | 4144.047 | 0.193 | 0.197 |
| age + animal rights + respondent ethnicity + character gender + people vs animals + trust in scientists + twitter usage | 32 | -2039.228 | 4144.186 | 0.332 | 0.184 |
| age + animal rights + respondent ethnicity + people vs animals + trust in scientists + twitter usage | 31 | -2040.474 | 4144.573 | 0.719 | 0.151 |
| age + animal rights + respondent ethnicity + human rights + people vs animals + trust in scientists + twitter usage + character nationality | 38 | -2033.647 | 4145.735 | 1.881 | 0.085 |
| age + animal rights + respondent ethnicity + human rights + people vs animals + trust in scientists + twitter usage + character expertise | 39 | -2032.590 | 4145.751 | 1.897 | 0.084 |
| age + animal rights + respondent ethnicity + character gender + people vs animals + trust in scientists + twitter usage + character nationality | 33 | -2038.979 | 4145.799 | 1.945 | 0.082 |

## Appendix S4.2. AIC weights table for question 2

Results of model selection process for question 2 after removing redundant and uninformative parameters, showing the top-supported model and all models within Δ2 $AIC_c$.

| **Model** | **df** | **logLik** | **$AIC_c$** | **delta** | **$AIC_w$** |
|---|---|---|---|---|---|
| Age + animal rights + respondent ethnicity + character expertise + human rights + people vs animals + character race + trust in scientists + twitter usage + character expertise * race | 42 | -2097.886 | 4282.742 | 0 | 0.350 |
| Age + animal rights + respondent ethnicity + character expertise + people vs animals + character race + trust in scientists + twitter usage + character expertise * race | 36 | -2104.528 | 4283.236 | 0.493 | 0.273 |
| Age + animal rights + respondent ethnicity + character expertise + people vs animals + character race + trust in scientists + twitter usage + character expertise * race + character gender | 37 | -2103.572 | 4283.446 | 0.704 | 0.246 |
| Age + animal rights + character expertise + human rights + people vs animals + character race + trust in scientists + twitter usage + character expertise * race | 37 | -2104.206 | 4284.715 | 1.972 | 0.131 |

## Appendix S4.3. AIC weights table for question 3

Results of model selection process for question 3 after removing redundant and uninformative parameters, showing the top-supported model and all models within Δ2 $AIC_c$.

| **Model** | **df** | **logLik** | **$AIC_c$** | **delta** | **$AIC_w$** |
|---|---|---|---|---|---|
| Animal rights + respondent ethnicity + character expertise + character gender + people vs animals + character race + trust in scientists + twitter usage + character expertise * race + character gender * race | 37 | -1904.137 | 3884.744 | 0 | 0.234 |
| Animal rights + character expertise + character gender + people vs animals + character race + trust in scientists + twitter usage + character expertise * race + character gender * race + character nationality + character nationality * race | 34 | -1907.924 | 3885.935 | 1.191 | 0.129 |
| Animal rights + character expertise + character gender + people vs animals + character race + trust in scientists + twitter usage + character expertise * race + character gender * race | 32 | -1910.065 | 3885.979 | 1.235 | 0.126 |
| Animal rights + respondent ethnicity + character gender + people vs animals + character race + trust in scientists + twitter usage + character gender * race | 33 | -1909.032 | 3886.030 | 1.286 | 0.123 |
| Animal rights + respondent ethnicity + character gender + people vs animals + character race + trust in scientists + twitter usage + character gender * race + character nationality + character nationality * race | 35 | -1906.964 | 3886.139 | 1.395 | 0.116 |
| Animal rights + respondent ethnicity + character gender + people vs animals + character race + trust in scientists + twitter usage + character gender * race + character nationality + character nationality * race | 34 | -1908.178 | 3886.443 | 1.699 | 0.100 |
| Animal rights + respondent ethnicity + people vs animals + trust in scientists + twitter usage | 30 | -1912.515 | 3886.655 | 1.911 | 0.090 |
| Animal rights + respondent ethnicity + character expertise + character gender + people vs animals + character race + trust in scientists + twitter usage + character gender * race | 35 | -1907.300 | 3886.810 | 2.066 | 0.083 |

## Appendix S5. Regression output for question 1

Summary of the ordinal regression results from the top-supported model for question 1 (to what extent do you agree that the information presented in Pat Rogers' pinned tweet is credible?) with coefficient estimates presented alongside the standard error, 85% confidence intervals, and p values. The baseline of reference for each categorical variable is as follows- Gender, Woman; People vs animals, Strongly prioritize animals; Animal rights, Strongly disagree; Human rights, Strongly disagree; Scientists, none at all; Twitter usage, Less than once a month; Ethnicity of respondent, White.

| Variable | Coefficient estimate | SE | CI (85%) | p |
|---|---|---|---|---|
| Gender, Man | 0.157 | 0.103 | 0.009, 0.305 | 0.128 |
| Animal rights, Disagree | 1.766 | 1.499 | -0.439, 3.917 | 0.239 |
| Animal rights, Somewhat disagree | 2.953 | 1.128 | 1.331, 4.599 | 0.009 |
| Animal rights, Neither agree nor disagree | 2.024 | 0.945 | 0.671, 3.423 | 0.032 |
| Animal rights, Somewhat agree | 2.416 | 0.931 | 1.085, 3.796 | 0.009 |
| Animal rights, Agree | 2.676 | 0.927 | 1.350, 4.050 | 0.004 |
| Animal rights, Strongly agree | 3.636 | 0.925 | 2.312, 5.005 | <0.001 |
| Human rights, Disagree | -0.521 | 1.514 | -2.814, 1.550 | 0.731 |
| Human rights, Somewhat disagree | 0.248 | 1.232 | -1.578, 2.016 | 0.840 |
| Human rights, Neither agree nor disagree | 1.455 | 0.825 | 0.275, 2.657 | 0.078 |
| Human rights, Somewhat agree | 1.835 | 0.789 | 0.707, 2.986 | 0.020 |
| Human rights, Agree | 1.696 | 0.779 | 0.582, 2.835 | 0.030 |
| Human rights, Strongly agree | 1.492 | 0.774 | 0.386, 2.625 | 0.054 |
| People vs animals, Prioritize animals | -0.815 | 0.182 | -1.078, -0.555 | <0.001 |
| People vs animals, Prioritize neither animals nor people | -1.360 | 0.196 | -1.643, -1.079 | <0.001 |
| People vs animals, Prioritize people | -1.459 | 0.201 | -1.748, -1.171 | <0.001 |
| People vs animals, Strongly prioritize people | -1.207 | 0.224 | -1.530, -0.885 | <0.001 |
| People vs animals, I don't know | -1.556 | 0.257 | -1.927, -1.186 | <0.001 |
| Scientists, A little | 0.577 | 0.360 | 0.060, 1.099 | 0.109 |
| Scientists, A moderate amount | 0.521 | 0.336 | 0.039, 1.009 | 0.121 |

| | | | | |
|---|---|---|---|---|
| Scientists, A lot | 0.964 | 0.338 | 0.479,  1.453 | 0.004 |
| Scientists, A great deal | 1.255 | 0.338 | 0.770,  1.746 | <0.001 |
| Scientists, I don't know | 0.734 | 0.523 | -0.018,  1.489 | 0.160 |
| Twitter usage, At least once a month | -0.075 | 0.245 | -0.428,  0.278 | 0.760 |
| Twitter usage, At least once a week | -0.055 | 0.212 | -0.360,  0.250 | 0.797 |
| Twitter usage, Every day | 0.454 | 0.212 | 0.148,  0.760 | 0.033 |
| Age | -0.010 | 0.003 | -0.015,  -0.005 | 0.002 |
| Ethnicity of respondent, Asian | 0.472 | 0.213 | 0.166,  0.779 | 0.027 |
| Ethnicity of respondent, Black | 0.750 | 0.281 | 0.347,  1.159 | 0.008 |
| Ethnicity of respondent, Mixed race | -0.226 | 0.339 | -0.715,  0.263 | 0.504 |
| Ethnicity of respondent, Any other ethnic group | -0.415 | 0.550 | -1.209,  0.387 | 0.451 |
| Ethnicity of respondent, Prefer not to say | -0.028 | 0.604 | -0.902,  0.850 | 0.962 |

## Appendix S6.1. Regression output for question 2

Summary of the ordinal regression results from the top-supported model for question 2 (to what extent do you agree with Pat Rogers that we should relocate people to protect lions?) with coefficient estimates presented alongside the standard error, 85% confidence intervals, and p values. The baseline of reference for each categorical variable is as follows- Race, Black; Expertise, Enthusiast; Animal rights, Strongly agree; Human rights, Strongly agree; People vs animals, Strongly prioritize animals; Scientists, None at all; Twitter usage, Less than once a month; Ethnicity of respondent, White.

| Variable | Coefficient estimate | SE | CI (85%) | p |
|---|---|---|---|---|
| Race, White | -0.300 | 0.179 | -0.559, -0.042 | 0.094 |
| Expertise, Field assistant | -0.214 | 0.174 | -0.465, 0.036 | 0.219 |
| Expertise, Professor | -0.437 | 0.177 | -0.692, -0.183 | 0.013 |
| Race, White*Expertise, Field assistant | 0.024 | 0.251 | -0.338, 0.386 | 0.924 |
| Race, White*Expertise, Professor | 0.727 | 0.251 | 0.367, 1.088 | 0.004 |
| Animal rights, Disagree | -1.395 | 1.421 | -3.677, 0.572 | 0.326 |
| Animal rights, somewhat Disagree | 0.641 | 0.969 | -0.738, 2.071 | 0.508 |
| Animal rights, Neither agree nor disagree | 0.762 | 0.826 | -0.403, 2.004 | 0.356 |
| Animal rights, Somewhat agree | 1.563 | 0.81 | 0.425, 2.784 | 0.053 |
| Animal rights, Agree | 1.761 | 0.807 | 0.627, 2.978 | 0.029 |
| Animal rights, Strongly agree | 2.680 | 0.807 | 1.547, 3.896 | 0.001 |
| Human rights, Disagree | 0.216 | 1.104 | -1.388, 1.810 | 0.845 |
| Human rights, Somewhat disagree | -1.263 | 1.380 | -3.506, 0.625 | 0.360 |
| Human rights, Neither agree nor disagree | 1.009 | 0.767 | -0.089, 2.131 | 0.188 |
| Human rights, Somewhat agree | 1.329 | 0.720 | 0.299, 2.386 | 0.065 |
| Human rights, Agree | 1.152 | 0.713 | 0.133, 2.199 | 0.106 |
| Human rights, Strongly agree | 0.928 | 0.708 | -0.084, 1.970 | 0.190 |
| People vs animals, Prioritize animals | -0.996 | 0.181 | -1.258, -0.736 | <0.001 |
| People vs animals, Prioritize neither animals nor people | -1.727 | 0.197 | -2.011, -1.445 | <0.001 |
| People vs animals, Prioritize people | -2.051 | 0.201 | -2.342, -1.763 | <0.001 |

| | | | | |
|---|---|---|---|---|
| People vs animals, Strongly prioritize people | -1.841 | 0.230 | -2.173, -1.512 | <0.001 |
| People vs animals, I don't know | -2.071 | 0.263 | -2.451, -1.694 | <0.001 |
| Scientists, A little | 0.257 | 0.377 | -0.283, 0.805 | 0.497 |
| Scientists, A moderate amount | 0.294 | 0.354 | -0.212, 0.810 | 0.407 |
| Scientists, A lot | 0.729 | 0.355 | 0.223, 1.246 | 0.040 |
| Scientists, A great deal | 0.928 | 0.355 | 0.421, 1.444 | 0.009 |
| Scientists, I don't know | 0.953 | 0.525 | 0.199, 1.714 | 0.070 |
| Twitter usage, At least once a month | -0.127 | 0.248 | -0.484, 0.229 | 0.608 |
| Twitter usage, At least once a week | 0.068 | 0.218 | -0.246, 0.382 | 0.755 |
| Twitter usage, Every day | 0.315 | 0.218 | 0.001, 0.628 | 0.148 |
| Age | -0.018 | 0.003 | -0.023, -0.014 | <0.001 |
| Ethnicity of respondent Asian | 0.534 | 0.209 | 0.234, 0.837 | 0.011 |
| Ethnicity of respondent Black | 0.500 | 0.287 | 0.086, 0.914 | 0.082 |
| Ethnicity of respondent Mixed race | 0.252 | 0.340 | -0.238, 0.743 | 0.459 |
| Ethnicity of respondent Any other ethnic group | -0.861 | 0.519 | -1.611, -0.106 | 0.097 |
| Ethnicity of respondent Prefer not to say | -0.226 | 0.586 | -1.086, 0.616 | 0.700 |

## Appendix S6.2. Tukey test for question 2

Summary of the Tukey test results for the interaction terms in the top-supported model for question 2 (to what extent do you agree with Pat Rogers that we should relocate people to protect lions?) with coefficient estimates presented alongside the standard error.

| Race | Expertise | Estimate | SE | df | Asymp.LCL | Asymp.UCL |
|---|---|---|---|---|---|---|
| Black | Enthusiast | 1.076 | 0.128 | Inf | 0.689 | 1.464 |
| White | Enthusiast | 0.776 | 0.132 | Inf | 0.376 | 1.176 |
| Black | Field assistant | 0.862 | 0.125 | Inf | 0.483 | 1.241 |
| White | Field assistant | 0.586 | 0.127 | Inf | 0.200 | 0.971 |
| Black | Professor | 0.639 | 0.127 | Inf | 0.255 | 1.024 |
| White | Professor | 1.066 | 0.126 | Inf | 0.684 | 1.448 |

## Appendix S7.1. Regression output for question 3

Summary of the ordinal regression results from the top-supported model for question 3 (to what extent do you agree that Pat Rogers is a trustworthy source of lion conservation information?) with coefficient estimates presented alongside the standard error, 85% confidence intervals, and p values. The baseline of reference for each categorical variable is as follows- Race, Black; Gender, Woman; Expertise, Enthusiast; Animal rights, Strongly disagree; People vs animals, Strongly prioritize animals; Scientists, none at all; Twitter usage, Less than once a month; Ethnicity of respondent, White.

| Variable | Coefficient estimate | SE | CI (85%) | p |
|---|---|---|---|---|
| Race, White | -0.012 | 0.216 | -0.322, 0.298 | 0.955 |
| Gender, Man | 0.320 | 0.149 | 0.106, 0.535 | 0.031 |
| Expertise, Field assistant | -0.112 | 0.181 | -0.372, 0.148 | 0.537 |
| Expertise, Professor | -0.116 | 0.185 | -0.383, 0.151 | 0.532 |
| Race, White*Expertise, Field assistant | 0.213 | 0.260 | -0.161, 0.587 | 0.413 |
| Race, White*Expertise, Professor | 0.646 | 0.262 | 0.268, 1.024 | 0.014 |
| Race, White*Gender, Man | -0.575 | 0.213 | -0.883, -0.268 | 0.007 |
| Animal rights, Disagree | 2.017 | 1.268 | 0.171, 3.840 | 0.112 |
| Animal rights, somewhat Disagree | 1.029 | 0.918 | -0.288, 2.365 | 0.262 |
| Animal rights, Neither agree nor disagree | 0.949 | 0.746 | -0.113, 2.047 | 0.204 |
| Animal rights, Somewhat agree | 1.891 | 0.723 | 0.864, 2.958 | 0.009 |
| Animal rights, Agree | 1.981 | 0.712 | 0.971, 3.033 | 0.005 |
| Animal rights, Strongly agree | 2.527 | 0.711 | 1.518, 3.579 | <0.001 |
| People vs animals, Prioritize animals | -0.834 | 0.185 | -1.101, -0.569 | <0.001 |
| People vs animals, Prioritize neither animals nor people | -1.285 | 0.199 | -1.572, -0.999 | <0.001 |
| People vs animals, Prioritize people | -1.159 | 0.199 | -1.446, -0.873 | <0.001 |
| People vs animals, Strongly prioritize people | -0.861 | 0.220 | -1.178, -0.545 | <0.001 |
| People vs animals, I don't know | -1.103 | 0.279 | -1.506, -0.701 | <0.001 |
| Scientists, A little | 0.789 | 0.385 | 0.236, 1.346 | 0.041 |
| Scientists, A moderate amount | 0.970 | 0.36 | 0.454, 1.492 | 0.007 |

|  |  |  |  |  |
|---|---|---|---|---|
| Scientists, A lot | 1.297 | 0.363 | 0.778,  1.823 | <0.001 |
| Scientists, A great deal | 1.493 | 0.361 | 0.976,  2.016 | <0.001 |
| Scientists, I don't know | 0.635 | 0.536 | -0.136,  1.411 | 0.237 |
| Twitter usage, At least once a month | 0.336 | 0.256 | -0.033,  0.705 | 0.190 |
| Twitter usage, At least once a week | 0.405 | 0.223 | 0.083,  0.726 | 0.070 |
| Twitter usage, Every day | 0.829 | 0.224 | 0.508,  1.152 | <0.001 |
| Ethnicity of respondent Asian | 0.445 | 0.211 | 0.142,  0.749 | 0.035 |
| Ethnicity of respondent Black | 0.587 | 0.301 | 0.156,  1.024 | 0.051 |
| Ethnicity of respondent Mixed race | -0.239 | 0.369 | -0.771,  0.294 | 0.517 |
| Ethnicity of respondent Any other ethnic group | -0.612 | 0.620 | -1.526,  0.271 | 0.324 |
| Ethnicity of respondent Prefer not to say | -0.935 | 0.630 | -1.844,  -0.016 | 0.138 |

## Appendix S7.2. Tukey test output for question 3

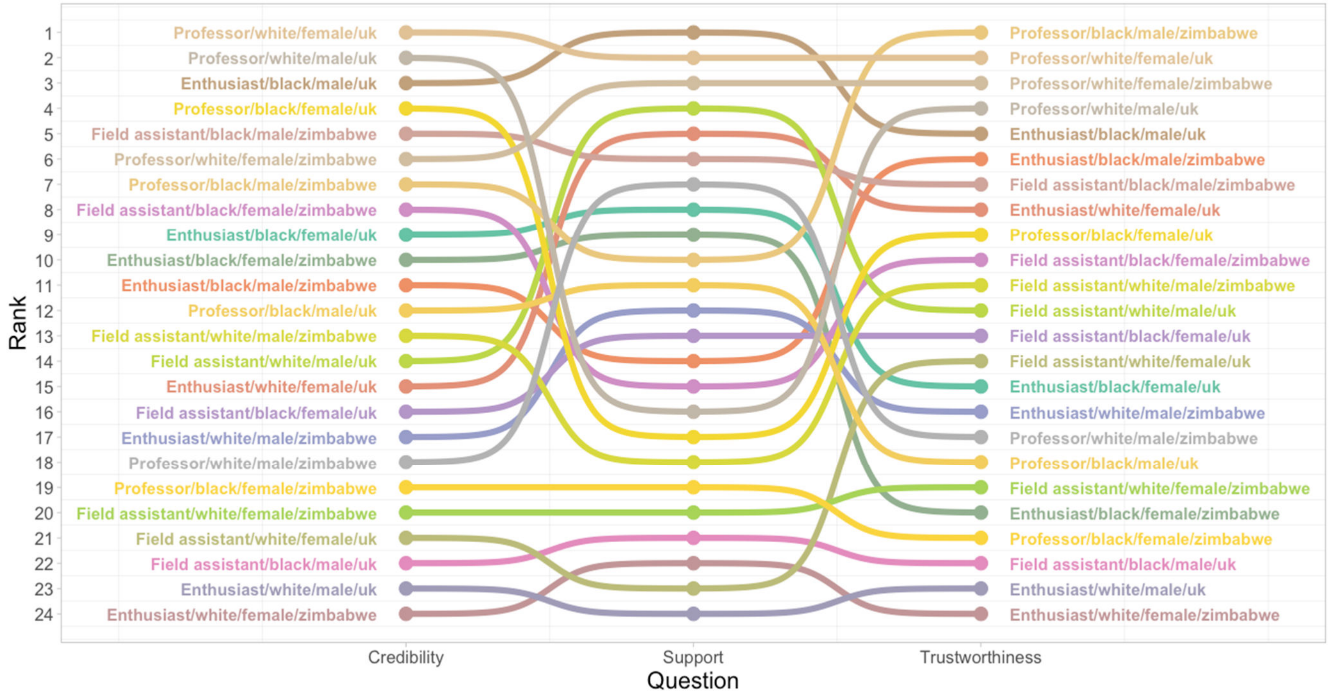
Summary of the Tukey test results for the interaction terms (race*expertise, and race*gender) in the top-supported model for question 3 (to what extent do you agree that Pat Rogers is a trustworthy source of lion conservation information?) with coefficient estimates presented alongside the standard error.

| Race | Expertise | Estimate | SE | df | Asymp.LCL | Asymp.UCL |
|---|---|---|---|---|---|---|
| Black | Enthusiast | 1.276 | 0.136 | Inf | 0.861 | 1.690 |
| White | Enthusiast | 0.974 | 0.137 | Inf | 0.558 | 1.389 |
| Black | Field assistant | 1.164 | 0.132 | Inf | 0.764 | 1.564 |
| White | Field assistant | 1.075 | 0.137 | Inf | 0.658 | 1.493 |
| Black | Professor | 1.160 | 0.137 | Inf | 0.744 | 1.575 |
| White | Professor | 1.504 | 0.137 | Inf | 1.088 | 1.919 |

| Race | Gender | Estimate | SE | df | Asymp.LCL | Asymp.UCL |
|---|---|---|---|---|---|---|
| Black | Woman | 1.038 | 0.111 | Inf | 0.727 | 1.350 |
| White | Woman | 1.315 | 0.118 | Inf | 0.984 | 1.646 |
| Black | Man | 1.359 | 0.114 | Inf | 1.039 | 1.678 |
| White | Man | 1.060 | 0.111 | Inf | 0.749 | 1.370 |

# Appendix S8. Change in rank position of each “Pat Rogers” character over the three research questions.

Plot shows the ranked position of the 24 versions of Pat Rogers (based on all possible combinations of the levels of expertise, race, gender, and nationality tested), from 1 (highest agreement) to 24 (lowest agreement) for each research question. Rankings were calculated based on overall percentage of responses in agreement (inclusive of somewhat agree, agree, and strongly agree), with higher percentage agreement increasing the ranking of the profile.



## Appendix S9. Extended Results and Discussion

### Extended results

Across all three research questions, and all 24 profiles, the greatest proportion of respondents were in overall agreement rather than disagreement, but there was considerable variation between profiles within each research question (see Figures 3a, 4a and 6a). The relative ranking of each version of Pat Rogers, based on the extent of respondent's agreement across the three research questions, showed considerable variability (Appendix S8). The only character that consistently ranked within the top 3 was the white, woman, British professor, while the only characters to consistently rank within the bottom 3 were the white, man, British enthusiast and the white, woman, Zimbabwean enthusiast.

### Credibility

The white, woman, British professor was viewed as the most credible source (81.1% of respondents either strongly agreeing, agreeing, or somewhat agreeing with the statement provided by this character). This character also had the highest number of participants strongly agreeing that the post was credible (32.1%). Overall, the white, woman, Zimbabwean enthusiast was perceived to be least credible (31.3% of respondents either strongly disagreeing, disagreeing, or somewhat disagreeing with their post). However, the Black, woman, Zimbabwean field assistant generated the highest proportion of respondents strongly disagreeing that the post was credible (9.8%; Figure 2a).

### Support

The Black, man, British enthusiast generated the most support (75.4% of respondents either strongly agreeing, agreeing, or somewhat agreeing). This character also had the highest number of participants strongly agreeing that people should be relocated to address human-lion conflict (31.6%). Overall, the white, woman, Zimbabwean enthusiast, generated the least support (43.7% of respondents either strongly disagreeing, disagreeing, or somewhat disagreeing). However, the white, woman, Zimbabwean, field assistant generated the biggest proportion of respondents strongly disagreeing that people should be relocated (12.0%).

### Trustworthiness

The Black, man, Zimbabwean professor was perceived as most trustworthy (76.4% of respondents either strongly agreeing, agreeing, or somewhat agreeing). However, the white, woman, Zimbabwean professor generated the biggest proportion of respondents strongly agreeing that Pat Rogers was trustworthy (34.7%). Overall, the Black, man, Zimbabwean enthusiast was perceived as least trustworthy (22.9% of respondents either strongly disagreeing, disagreeing, or somewhat disagreeing). However, the Black, woman, British professor generated the biggest proportion of respondents strongly disagreeing that Pat Rogers was trustworthy (9.6%).

## Extended discussion

We chose to explore these questions using X as the platform for conservation information dissemination, primarily because it facilitated the seamless display of a conservation message (via the pinned post) beside the identity details we manipulated in the biography. This provided a unique set up that would be difficult to replicate via other social media platforms or news outlets.

We further chose to contextualize the study within the field of lion conservation due to the charismatic status of the species. Recently there has been considerable news coverage surrounding lion conservation in the UK, specifically focused on trophy hunting bans (Yeomans et al., 2022). While we did attempt to control for discrepancies in individual knowledge of lion conservation by providing an objective statement at the start of the survey (Appendix S1), it is possible that existing opinions will have influenced participants' responses. Overall, most respondents agreed with the credibility of the lion conservation information, supported its implementation, and trusted the conservationist as a source of information. It would be interesting to conduct a similar study using a less charismatic species, or using a message that generated less public support, to investigate what effect these factors have on identity- bias.

With increasing age, both perceived credibility and support for the conservationist’s recommendation decreased. This could be due to greater skepticism towards scientific information on X amongst older demographics, or a skepticism towards trusting information communicated by individuals younger than themselves.

The ethnicity of participants influenced their response to each of our research questions. We interpret these results with caution because of the low sample sizes within several of the ethnic groups (due to stratifying the respondent pool to match the UK population). In future it would be helpful to sample equally across ethnic groups to facilitate a more detailed analysis of these effects.

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**Author for correspondence:**
Lauren F. Rudd
e-mail: lauren.rudd@gtc.ox.ac.uk

# Overcoming racism in the twin spheres of conservation science and practice

Lauren F. Rudd[1,2,†], Shorna Allred[4,5], Julius G. Bright Ross[1,2], Darragh Hare[1,2,4], Merlyn Nomusa Nkomo[6], Kartik Shanker[7,8], Tanesha Allen[1], Duan Biggs[9], Amy Dickman[1,2,10], Michael Dunaway[11], Ritwick Ghosh[12], Nicole Thompson González[13], Thembela Kepe[14,15], Moreangels M. Mbizah[16,17,18], Sara L. Middleton[1,3], Meera Anna Oommen[8], Kumar Paudel[19,20], Claudio Sillero-Zubiri[1,2,21] and Andrea Dávalos[22]

[1]Department of Zoology, [2]Wildlife Conservation Research Unit, and [3]Department of Plant Sciences, Oxford University, UK
[4]Center for Conservation Social Sciences, Department of Natural Resources and the Environment, and
[5]Department of Global Development, Cornell University, USA
[6]Fitzpatrick Institute of African Ornithology, University of Cape Town South Africa, Cape Town, South Africa
[7]Centre for Ecological Sciences, Indian Institute of Science, India
[8]Dakshin Foundation, India
[9]Environmental Futures Research Institute, Griffith University, Australia
[10]Lion Landscapes, Tanzania
[11]Department of Sociology, Syracuse University, USA
[12]Global Futures Laboratory, Arizona State University, USA
[13]Department of Anthropology, University of New Mexico, USA
[14]Department of Geography, University of Toronto, Canada
[15]Geography Department, Rhodes University, South Africa
[16]Wildlife Conservation Action, Zimbabwe
[17]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland
[18]Sustainability Research Unit, Nelson Mandela University, George, South Africa
[19]Greenhood Nepal, Nepal
[20]Department of Geography, University of Cambridge, UK
[21]Born Free Foundation, Ethiopia and UK
[22]Biological Sciences Department, SUNY Cortland, USA

LFR, 0000-0002-5925-9514; SA, 0000-0001-6237-0638; JGBR, 0000-0003-2454-1592; DH, 0000-0003-4418-9637; MNN, 0000-0002-0609-0153; KS, 0000-0003-4856-0093; NTG, 0000-0002-3195-1277; TK, 0000-0002-1807-0387; MMM, 0000-0002-6868-052X; SLM, 0000-0001-5307-8029; AD, 0000-0002-3590-4152

It is time to acknowledge and overcome conservation's deep-seated systemic racism, which has historically marginalized Black, Indigenous and people of colour (BIPOC) communities and continues to do so. We describe how the mutually reinforcing 'twin spheres' of conservation science and conservation practice perpetuate this systemic racism. We trace how institutional structures in conservation science (e.g. degree programmes, support and advancement opportunities, course syllabuses) can systematically produce conservation graduates with partial and problematic conceptions of conservation's history and contemporary purposes. Many of these graduates go on to work in conservation practice, reproducing conservation's colonial history by contributing to programmes based on outmoded conservation models that disproportionately harm rural BIPOC communities and further restrict access and inclusion for BIPOC conservationists. We provide practical, actionable proposals for breaking vicious cycles of racism in the system of conservation we have with virtuous cycles of inclusion, equality, equity and participation in the system of conservation we want.

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[†]Present address: Green Templeton College, 43 Woodstock Road, Oxford, OX2 6HG, UK.

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## 1. Introduction

It is time to acknowledge and overcome conservation's deep-seated systemic racism, which has historically marginalized Black, Indigenous and people of colour (BIPOC) communities, and continues to do so [1–5]. Given conservation's history of racism, exclusion and oppression [1,6], and the fundamental role that BIPOC communities must play in biodiversity conservation, conservation researchers and practitioners must lead the way in committing to anti-racism [7]. Failing to examine, acknowledge and act on persistent oppression in our field provides tacit support to racism, tarnishing the conservation successes we achieve, and causing real harm to some of the world's most vulnerable people [8].

In this paper, we critique contemporary mainstream conservation: formalized, evidence-based efforts to conserve biodiversity. Despite its relatively brief history, this form of conservation globally dominates indigenous knowledge systems through which people have actively and adaptively conserved ecosystems for millennia [9]. In many places, mainstream conservation has replaced indigenous knowledge systems, often to the detriment of local people and biodiversity [10].

We draw on existing literature and our interdisciplinary, cross-sectoral, professional experiences to identify issues of and propose solutions to systemic racism in what we term the 'twin spheres' of conservation: (i) 'conservation science': academic teaching and research, which typically takes place on college and university campuses and (ii) 'conservation practice': applied conservation policies and programmes, which typically take place outside the campus gates. We argue that systemic racism mars our activities in these twin spheres of conservation science and practice, and that what we do in each sphere affects what happens in the other (figure 1). Conservation practice's colonial origins and racist history influence how academia conceptualizes conservation problems and solutions, what is taught, and the nature of interactions between students, colleagues and the local people on whose land research is conducted [1]. The racism that permeates the academic sphere is reproduced in conservation activities outside academia, in the biases and preconceptions that conservation graduates carry with them and apply to on-the-ground decision making in the organizations for which they work. In turn, these on-the-ground decisions affect conservation practice by influencing which conservation problems are addressed, how they are addressed and how colleagues and collaborators are treated. Conservationists' formal and informal practices can, often implicitly or unintentionally, impart racist and neo-colonialist undertones onto academic work (e.g. publications, conference presentations, teaching) which underpins many of the conservation programmes and policies that are studied and taught to subsequent cohorts of students (figure 1).

This vicious cycle in the twin spheres of conservation science and practice characterizes the conservation we have created and inherited, but it does not characterize the conservation we want. We urge fellow members of the conservation community—academics and practitioners—to take stock of the manner in which much of what we do in conservation science and practice perpetuates, reinforces and deepens racial divisions [1], and reflect honestly on how we can change our behaviours and institutions for the better. We are morally obliged to demolish racist structures, reform our individual and collective actions, and construct a more equal, inclusive and socially just field. We owe this to the people whom conservation has harmed and continues to harm, the communities on whose land we are privileged to work, the students we mentor and the broader societies we serve. We recognize and strongly welcome many recent steps in the right direction, but we have a long way to go.

We, the authors, are a diverse team representing, other than race, different ethnicities, levels in academia, years of experience in both conservation research and practice, primary fields of study and specializations in conservation, organizational affiliations and regions of the world. While we do not purport to speak for all conservationists in our different communities, the varied perspectives we discuss here represent our lived experiences and are not appropriated knowledge.

We acknowledge that the experiences of BIPOC individuals in conservation will depend on political, social and economic factors such as nationality, native language and socio-economic status. While the extent of racism faced by individuals and the obstacles they encounter may vary, BIPOC individuals are, on the whole, a minority within the conservation space. We also acknowledge that the state of conservation varies around the world. In some previously colonized countries, white western organizations, individualism and ideals still largely dominate conservation, but in other countries, local and regional efforts predominate. Even where BIPOC individuals currently lead conservation research and practice, these individuals often seem to come from positions of relative privilege within society, regardless of whether the society is BIPOC majority or BIPOC minority. To truly reconcile the historic racial injustices within the field of conservation, this type of privilege needs to be acknowledged and addressed.

Without recognizing barriers to individuals such as socio-economic background, language, access to training and networking opportunities, simply increasing the representation of BIPOC people in conservation will not solve the problem, as being a BIPOC individual does not guarantee either cultural literacy or an anti-racist outlook. Racist hierarchies and processes operate within every society and at multiple levels, not simply at the global scale of colonial legacy. While much of this conversation is outwith the scope of this paper, what we advocate for above all is fostering greater inclusivity within conservation, which should go some way towards addressing all the problems outlined.

## 2. Conservation practice's deep-seated racist history

Many dominant conservation tools, such as protected areas and quotas for sustainable use, are rooted in colonial strategies for optimizing resource extraction and recreational opportunities on colonized land [11,12]. These practices came at great cost to local people, including through forced removal, abuse, loss of livelihoods, cultural assimilation, human rights abuses and death [13–15]. For example, Native American people were killed or forcibly removed from their ancestral lands to create national parks that appealed to settler colonists' wilderness ideals [13,16]. Long-standing indigenous and local cultural practices, norms and taboos were replaced by extractive or preservationist values of European colonists [9,17,18]. Contemporary conservation can perpetuate these values, often in spite of strenuous opposition from Indigenous and local people [19].

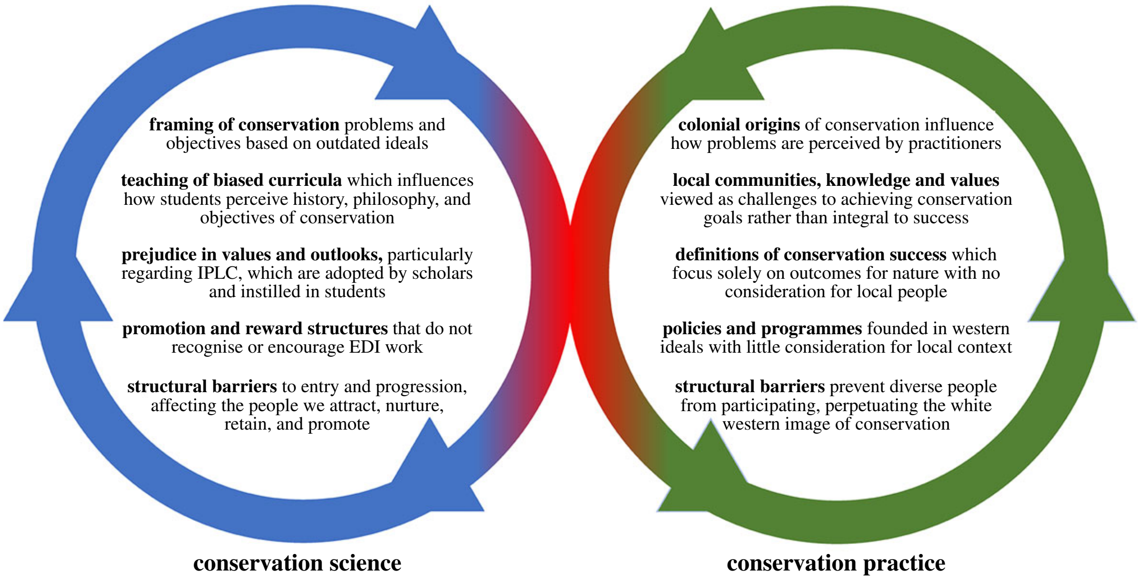

**Figure 1.** The mutually reinforcing twin spheres of conservation science and conservation practice. Although each sphere can operate largely independently of the other, they each perpetuate neo-colonial and racist ideologies that reinforce the other in subtle but important ways. Escaping this vicious cycle will require conservation scientists and practitioners to change our individual and collective behaviours (boxes 1–3). Definitions: Indigenous peoples and local communities (IPLCs); equality, diversity and inclusion (EDI). (Online version in colour.)

While extractive approaches can be clearly neo-colonial and racist, preservationism can be less obviously so. The preservationist approach seeks to preserve 'Eden'-like environments, often via protected areas [12,18]. Recognizing the extent of ecological degradation across much of the Global North, advocates of this approach appear to believe that conservation can only happen elsewhere in pristine environments, typically in the Global South. Preservationist efforts may be well-intentioned (e.g. by seeking to protect critically endangered populations or areas of high biodiversity) but are often blind to the environmental injustices they impose on local people through fortress conservation (conservation through formal, exclusionary protected areas, that displace and marginalize local people and prioritize the interests of wealthy, often distant, elites) [20]. In our experience, conservationists from the Global North often lack local cultural literacy and come equipped with the privileged legacy of colonial power, perpetuating a 'white saviour' mentality [21]. Related tensions are evident in 'parachute science', in which external conservationists suddenly arrive in a new place to conduct research, using local scientists only as field staff or data collectors under the pretext that local capacity or expertise is lacking [22,23]. Some of the best-known examples of conservation practice, as well as many academic conservation scientists' field experiences, are enmeshed in such unjust paradigms. When academics bring these examples and experiences uncritically into formal and informal teaching, conservation students may internalize them as normal or desirable.

Conservation's colonial underpinnings continue to permit practices that subjugate local people by portraying them as responsible for conservation problems, forcibly removing them from their land in the name of conservation and preventing them from accessing wildlife and protected areas [6,8,24], often by militarized means [25,26]. Some influential researchers and advocacy groups based in the Global North advocate for extending their preferred conservation ideologies to vastly different socioecological and cultural contexts, with apparently little regard for traditional practices or ethics in those locations [15]. Such prescriptions can endorse social hierarchies (e.g. caste in India) by privileging certain practices (e.g. vegetarianism) without understanding the historical and social inequities associated with them [27]. More broadly, these practices disempower people in the Global South by demanding they change their behaviours, many of which they have been practising for millennia, to suit the preferences of distant interest groups. Such demands are particularly distasteful when couched, seemingly without irony, in anti-colonial and pro-equality rhetoric [28]. High-profile proposals to increase the amount of land and seascapes designated as exclusionary protected areas (e.g. [29]) show little consideration for social and cultural consequences [30]. Western interests claiming or maintaining de facto control over many conservation spaces in the Global South is straightforward neo-colonialism [31], a contemporary form of land grabbing permitted in the name of environmental protection [32].

## 3. Exclusion from engaging with nature

The high degree of exclusion of BIPOC people across levels of conservation science and practice reproduces conservation practice's colonial history. Many BIPOC people have been excluded from environmental policymaking. The ability for indigenous communities to effectively participate in policies that affect them has been removed through colonial processes in many parts of the world. For example, the Marshall Trilogy of Supreme Court decisions (Johnson v. M'Intosh 1823, Cherokee Nation v. Georgia 1831, and Worcester v. Georgia 1832) in the United States, the Treaty of Waitangi (1840) in New Zealand, and the policy of Terra Nullius in Australia (1835), all placed Indigenous sovereignty over land and resources within the dominion of colonial governments.

In BIPOC minority countries, people of colour are further excluded from conservation because they are less likely to

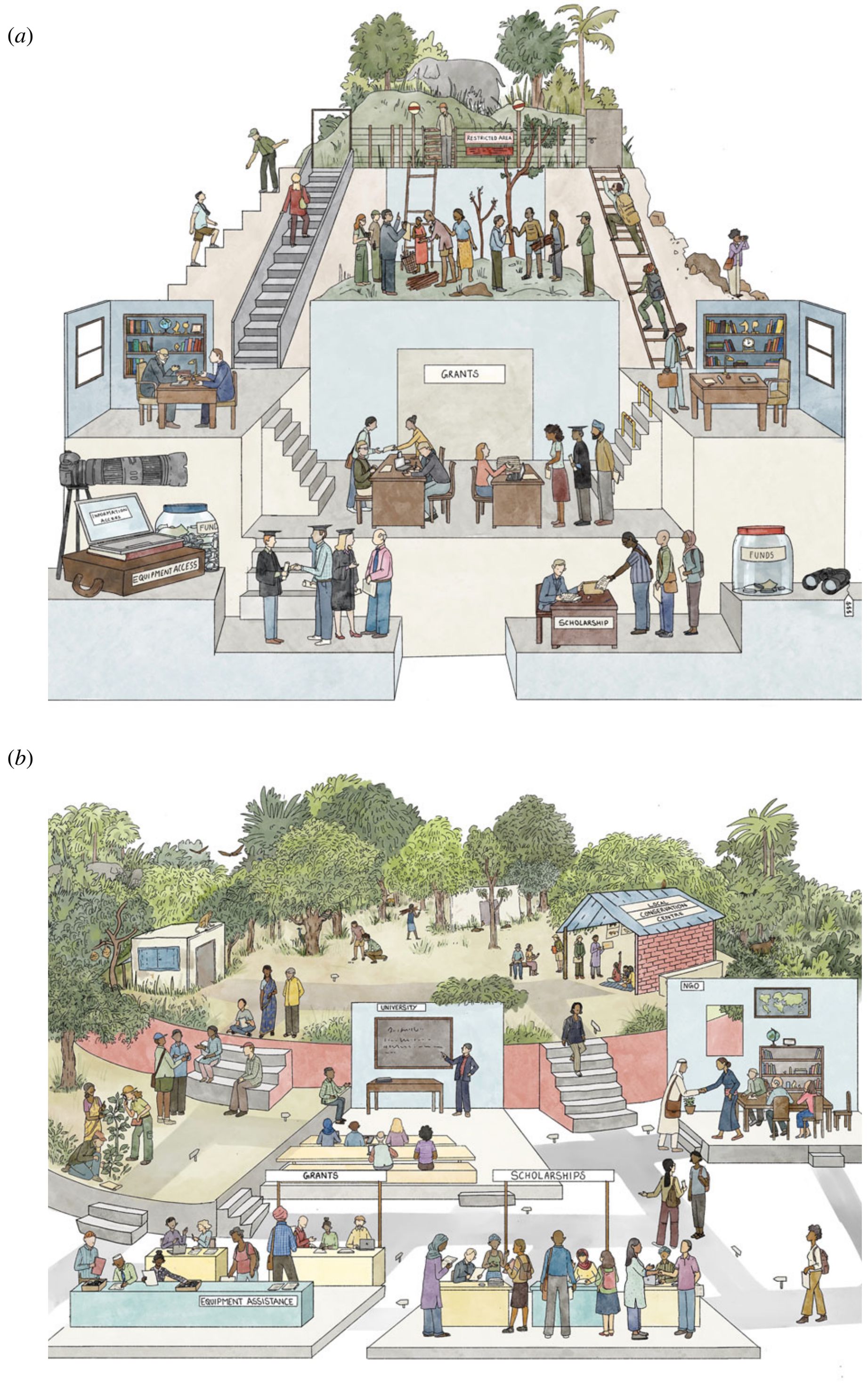

**Figure 2.** The conservation we have (*a*) and the conservation we want (*b*). Current pathways to success systematically favour some groups over others. Each step in the academic process represents a successive impediment to aspiring BIPOC conservationists, from the resources to pursue such a career, to the attentiveness of supervision received, to the degree of welcome that recent graduates of different skin colours receive in the industry. Consequently, conservation practice is designed and communicated to local people by outsiders who may fail to understand local context or are beholden to predominant western approaches to conservation. We must strive to bring about a system that is more attractive and more accessible to BIPOC aspirants. The academic system should only represent one valid entry point to conservation. By enabling the sharing of expertise from local conservationists and increasing career mobility between field conservation, academia and the non-profit sector, multiple stakeholder viewpoints can be prioritized in the process of moving towards more holistic, novel models of conservation. Illustration by Barkha Lohia. (Online version in colour.)

have access to and use outdoor spaces for recreational purposes than people from predominantly white communities [33,34]. Recent high-profile cases in the United States and United Kingdom demonstrate that people of colour, and particularly Black people, are often unsafe and unwelcome in outdoor spaces [35,36].

Exclusion is also evident in financial hurdles to entering conservation, particularly for many from BIPOC communities

**Box 1.** How to recognize and address the unjust history of conservation science.

1. Educate oneself on the history of racism in conservation through reading, reflecting on one's own experiences and engaging in dialogue with others. Recommended reading [6,11–13,16,20,31].
2. Diversify and broaden the curriculum; teach a more comprehensive representation of past and present conservation practice, including the work and perspectives of BIPOC scholars, and ultimately produce new 'standard' textbooks that encompass this history. Recommended reading [2,59–63].
3. Prioritize inclusive teaching practices in conservation courses by embracing the tenets of inclusive course design, active learning modalities and service learning techniques, to encourage broader participation and interest in conservation sciences. Recommended reading [64–67].
4. Conduct outreach in predominantly BIPOC schools and areas within predominantly white countries to promote conservation careers at an early age. Potential outreach activities could include hands-on activities, 'meet a conservation scientist' Q&A session, talks at school career days and hosting research events tailored for high school students.
5. Encourage professional associations to fully integrate equity, diversity and inclusion (EDI) into their policies and standards, (for example, the Society for Conservation Biology should update their guidelines for conservation literacy to include a section on EDI).
6. Question dominant narratives about what works in conservation, including how success is measured, and track the history of power relations shaping such narratives.
7. Recognize that injustice is not only historic or organizational, but occurs today within each of our lives. Challenging conversations, personal reflection and honesty are required for each of us to take personal, immediate steps to ensure we are not perpetuating unjust actions.
8. Understand that facing past wrongs is not just about rehashing the past, but to be honest about the present and to create a solid foundation for future action.

with a long history of economic exclusion. As examples, activities such as birding, diving and hiking to name a few require equipment that is often costly [37]. This financial barrier can be further amplified in some areas of the Global South if such equipment is not locally available or affordable, making it difficult to source. Because experience builds passion for the outdoors, inspiring people to pursue careers in conservation, socio-economic barriers block many BIPOC people's routes into conservation science and practice. Exclusion can be concentrated in certain sub-communities: individuals of different genders, migration experience and wealth within a recognized ethnic minority group may vary widely in their motivations and ability to use and interact with outdoor spaces [38]. BIPOC members of other minority communities may face additional barriers to safely using outdoor spaces [39,40]—experiences which can be compounded by racism. Further, colourism exacerbates the threat to dark-skinned BIPOC individuals, and the discrimination they face [41]. These converging forms of discrimination illustrate the magnitude and diversity of obstacles that systematically divert BIPOC people away from conservation (figure 2).

## 4. Racism in conservation science and practice today

Power in conservation typically resides in governments, corporations, large NGOs and universities [42]. Universities are central because they provide the qualifications required for a degree in conservation. However, BIPOC students are disproportionately underrepresented in degree subjects that lead to conservation careers [5,43,44], partly due to high upfront degree costs and lack of scholarships, expensive field trips, unpaid summer field experiences, low job security and the predominance of low-paid or voluntary entry-level positions [45]. Once enrolled, students are expected to undertake conservation work during summers and academic holidays to boost their credentials. However, field-based educational experiences may not always be designed with inclusivity in mind [46] and can perpetuate neo-colonial attitudes when being run by institutions outside the host country [47], making the experiences unsafe and uncomfortable for BIPOC students. Internship opportunities in universities, NGOs, governmental and intergovernmental agencies often target students from wealthier countries and are typically both expensive to enrol in and unpaid, thus carrying substantial transaction and opportunity costs [48,49]. Many BIPOC students cannot participate for financial or cultural reasons, missing out on valuable work experience, networks and job opportunities. Expectations that students hoping to work in conservation should go above and beyond and not expect a financial reward for their efforts, excludes many.

The predominant narrative of conservation taught in academia uncritically emphasizes the Western paradigm of pristine wilderness and fortress conservation, what Shanker & Oomen [31] term 'pristianity' named for the religious zeal in which preservation of wild spaces is pursued. Students in conservation degrees typically do not learn the colonial and deeply racist intentions and consequences of fortress conservation. Local knowledge is often referred to in passing as 'indigenous knowledge systems', relegating it to superstition and alternative thought while western ideas are imposed as the only way of understanding or engaging with ecosystems. Teaching this sanitized history of conservation perpetuates deep inequalities in the field and can alienate BIPOC students [50].

Advanced degrees are essential for many high-level conservation jobs, but funding for postgraduate study is scarce and predominantly flows to white students. For example, in

**Box 2.** How to construct better ways to conduct research and practice conservation.

1. Develop qualifying assessments for individuals to demonstrate 'cultural literacy' in relation to fieldwork sites (deliverables could be to incorporate local history, expected socio-economic impact, plans for local collaboration and plans for preventing neo-colonial relations in project proposals).
2. Ensure fair dissemination of funds and grants to BIPOC academics, conservation practitioners and BIPOC led organizations.
3. Develop new models to ensure that BIPOC voices are heard: e.g. balancing expensive, in-person networking events with opportunities for online networking (while being considerate of any technological barriers), to enable more participation from diverse conservationists.
4. Avoid 'parachute science'; meaningfully include local partners in conservation from question formulation and applied practice all the way through to publication and beyond (this applies to academic research and work done by NGOs and government agencies). For example, journals and funding bodies could require inclusion of local partners as co-authors or require a report of actions implemented to ensure inclusivity and equity when conducting research abroad [68].
5. Create opportunities for community members to have real agency in conservation projects and promote conservation management solutions that align with the communities' culture and values, even when those might conflict with the views of NGOs or other external stakeholders.
6. Respect the rights of Indigenous People and local communities to manage, benefit from, and sustainably use their resources, embracing—not suppressing—diverse conservation ethics and resource management systems.
7. Recognize that BIPOC communities are diverse and heterogeneous and have different values and cultures.
8. Promote bottom-up conservation practices that decentralize management practices and decision making. To do this, practitioners should embrace the core concepts from participatory action research, community-based research and indigenous methodologies, all of which focus on rebalancing power dynamics [69–75].
9. Collaborate with colleagues in history, political ecology, geography and other cognate disciplines to ensure inclusion of a broader perspective within conservation curricula, and that we consider critical perspectives throughout research design and implementation.

**Box 3.** How to create an inclusive, safe conservation that welcomes BIPOC individuals and allows them to thrive in conservation science and practice.

1. Ensure that 'essential' work experience is incorporated into undergraduate and graduate conservation degree programmes, is fully funded at this stage and is not used as a metric to judge candidates during admissions processes to these programmes, as they do not represent candidates' abilities but rather their opportunities.
2. Evaluate current harassment reporting and risk assessment procedures to ensure they protect anonymity and allow for reporting of issues specific to BIPOC individuals.
3. Recognize and reward EDI work in the same way we would traditional academic achievements.
4. Advocate for and actively create opportunities for your BIPOC colleagues, even when this means personally stepping aside/turning down opportunities.
5. Extend current EDI initiatives (e.g. for gender equality) to be inclusive of BIPOC individuals who also fall within the remit [76].
6. Protect BIPOC people in your team—learn through independent research and training programmes how, where and why they may be vulnerable. Listen with humility and compassion to their expressed concerns. Further, prevent their possible harm by, for example, creating a risk management plan for fieldwork, including mitigating strategies [39].
7. Learn the cultural histories, norms and values of the communities on whose land you conduct research, and incorporate them into your conservation. Include local people as partners to help define, measure and evaluate success.

the 2018–2019 application cycle for postgraduate study funding in the UK, only 6% of Natural Environment Research Council (NERC) studentships were awarded to ethnic minorities [51]. In the UK, success for white principal investigators applying to NERC for funding awards was 13% higher than for individuals from ethnic minorities [51]. Senior positions in environmental organizations are typically held by white people: as of 2014, people from minoritized ethnic groups occupied less than 12% of these leadership positions in the US [52]. Insular hiring practices such as advertising positions internally and developing unpaid internships into paid positions or degree scholarships exacerbate the problem.

Postgraduate study can be daunting, particularly to first-generation students, and BIPOC students disproportionately fall into this category [53]. In the light of this, respectful, supportive relationships between postgraduate students and their supervisors are pivotal to success. People generally prefer to work with those that they can relate to and have a common culture with—a concept known as 'affinity bias' [54], which can be compounded by colourism [55], and further disadvantage BIPOC students in a field dominated by white people. Costs of attending international conferences and publishing scientific articles, which are both crucial for career advancement, can pose prohibitive financial barriers. Such factors are compounded by additional barriers such as visa processes and expenses to exclude people from BIPOC-majority countries from studying overseas [56].

This series of obstacles (figure 2) to success means BIPOC researchers are woefully underrepresented in conservation science and practice, and those who remain have few opportunities for advancement. Lack of high-level representation means little consideration is given to the specific problems that BIPOC people encounter in trying to succeed within conservation. We have personally witnessed or experienced many of these problems in our own workplaces. We have observed how the unique welfare and safety challenges to BIPOC conservationists, both in the field and in the workplace [39], can be invisible to senior colleagues who are unaffected by them and cannot relate. Racial stereotypes and derogatory language are used too often when discussing local communities and field staff, which alongside relentless assumptions about where one is 'really from' when referring to colleagues of colour, further alienates BIPOC people. Further, 'old-boy' networks and low turnover of individuals in senior positions mean that encountering racism and discrimination remains common [50]. The burden of calling out and reporting such incidents often falls on BIPOC people, which is especially daunting to those in junior positions because harassment reporting procedures in organizations with few possible BIPOC complainants cannot guarantee anonymity.

Academia is not the only route into conservation, but it currently acts as the main gatekeeper. Other entry forms (such as on-the-ground experience, often held by local conservation workers) may actually equip people with many more useful skills and fewer harmful biases. However, broadly speaking from our collective experience, a lack of academic qualifications (sometimes compounded by language barriers) prevents people from being able to progress to higher level positions in organizations where decision-making power resides. Among development fields, conservation appears to have an almost 'Brahminical' reverence for academic qualifications. As such, and despite a greater emphasis on BIPOC people and communities in the last two decades, conservation narratives remain dominated by western and/or privileged biologists and elite international and local NGOs [31,42].

## 5. Building inclusive conservation science and practice

Diversifying conservation has both ethical and practical consequences; it is socially just and can improve the success of conservation initiatives. It is important for conservation scientists and practitioners to acknowledge that, historically, BIPOC communities most impacted by environmental issues have been the least included in decision making [10]. Continuing to perpetuate these unjust power dynamics will wreak havoc on some of the world's most vulnerable communities [8]. Legitimate participation of local people produces better conservation outcomes because it builds community capacity and provides the opportunity for members to be involved in the definition of the problem, the development of policies and the implementation of measures and evaluation, ultimately increasing project sustainability [57]. Diversifying conservation teams increases the breadth of perspectives, driving innovation [58]—innovations that are sorely needed for developing ecologically and socio-culturally sustainable conservation strategies. Most importantly, respecting the rights of Indigenous People and local communities is required by international law, and as such is an imperative, not an optional luxury [8].

It is incumbent on all members of the conservation community to recognize and address the unjust history of conservation (box 1). For example, we must recognize that some of the earliest proponents of environmental protection in the Global North and South were also ardent proponents of colonial expansion, eugenics and white supremacy. We must acknowledge this context while dismantling it and seeking solutions rooted in a system of inclusivity and equality. It is essential that we reflect on the ways in which we have personally harmed or disadvantaged people from BIPOC communities in our professional lives. Holding ourselves accountable and taking steps to rectify these wrongs is a vital first step towards creating a more inclusive and just conservation. This sense of individual responsibility should be the basis for building future conservation solutions.

Many people from BIPOC communities are interested in conservation but are often excluded and alienated from it due to historic, unequal power and privilege structures. These structures must fall. It is therefore essential that all members of the conservation community play an active role in replacing the conservation we have with the conservation we want (figure 2). This means rethinking our individual and collective behaviours to create more inclusive institutions and organizations (box 2) and making conservation a field in which BIPOC communities can be safe and thrive (box 3).

## 6. Conclusion

Achieving excellence in conservation practice and promoting equity, diversity, inclusion and justice in conservation science are not mutually exclusive. Rather, they are all crucial to creating effective conservation practices that empower BIPOC communities by reforming our conservation institutions in both spheres. Conservation scientists who are also conservation practitioners are at the nexus of the twin spheres, and as such have both the greatest potential and responsibility to create positive change. We recognize that many individuals, organizations and groups are taking meaningful steps towards modes of conservation that empower BIPOC communities [1–4,59,60,77,78]. Nevertheless, there is still more to be done, and we must accelerate away from the exclusive and harmful institutions we have inherited, towards more inclusive and innovative institutions that promote conservation spaces in which people and nature thrive (figure 2). While some individuals have more power than others to affect change, every person can play a role in building conservation spaces that empower BIPOC communities.

We challenge all members of the conservation community, including ourselves, to use whatever privilege we have to make progress, however, small. We need to speak out against injustices, small or large, recruit those who are less privileged, promote them, give them a platform or step aside so they can have ours. We need to change our syllabus and teach the difficult, shameful, aspects of conservation. We must acknowledge that some purported conservation successes come at an enormous and unconscionable cost to BIPOC communities and help prevent conservationists from committing similar errors in future. We need to strive to find that one inch of progress and then leverage it for systemic change. We must work within our spheres of influence to foster institutional change in research, practice, curricula, community partnerships, recruitment and retention, mentoring, and beyond.

Data accessibility. This article has no additional data.

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All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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## References

1. Chaudhury A, Colla S. 2021 Next steps in dismantling discrimination: lessons from ecology and conservation science. *Conserv. Lett.* **14**, e12774. (doi:10.1111/conl.12774)
2. Miriti MN, Bailey K, Halsey SJ, Harris NC. 2020 Hidden figures in ecology and evolution. *Nat. Ecol. Evol.* **4**, 1282. (doi:10.1038/s41559-020-1270-y)
3. Schell CJ, Guy C, Shelton DS, Campbell-Staton SC, Sealey BA, Lee DN, Harris NC. 2020 Recreating Wakanda by promoting Black excellence in ecology and evolution. *Nat. Ecol. Evol.* **4**, 1285–1287. (doi:10.1038/s41559-020-1266-7)
4. Tseng M, El-Sabaawi RW, Kantar MB, Pantel JH, Srivastava DS, Ware JL. 2020 Strategies and support for Black, Indigenous, and people of colour in ecology and evolutionary biology. *Nat. Ecol. Evol.* **4**, 1288–1290. (doi:10.1038/s41559-020-1252-0)
5. Cronin MR *et al*. 2021 Anti-racist interventions to transform ecology, evolution and conservation biology departments. *Nat. Ecol. Evol.* **2021**, 1213–1223. (doi:10.1038/s41559-021-01522-z)
6. Mbaria J, Ogada M. 2016 *The big conservation lie: the untold story of wildlife conservation in Kenya*. Auburn, WA: Lens & Pens Publishing.
7. King L. 2016 Black history as anti-racist and non-racist: an examination of two high school Black history textbooks. In *But I don't see color: the perils, practices, and possibilities of antiracist education*, pp. 63–79. Sense Publishers.
8. Mbizah M *et al*. Submitted. Do black lives matter in conservation? *Nature*.
9. Berkes F. 2017 *Sacred ecology*, 4th edn. London, UK: Taylor and Francis Inc.
10. Consortium ICCA. 2021 *Territories of Life: 2021 Report*. See report.territoriesoflife.org.
11. Grove RH. 1995 *Green imperialism: colonial expansion, tropical island edens and the origins of environmentalism, 1600–1860*. Cambridge, UK: Cambridge University Press.
12. Jepson P, Whittaker RJ. 2002 Histories of protected areas: internationalisation of conservationist values and their adoption in the Netherlands Indies (Indonesia). *Environ. Hist. Camb.* **8**, 129–172. (doi:10.3197/0967340 02129342620)
13. Kantor I. 2007 Ethnic cleansing and America's creation of national parks. *Public L. Resour. Law Rev.* **28**, 41–64.
14. Kashwan P, V. Duffy R, Massé F, Asiyanbi AP, Marijnen E. 2021 From racialized neocolonial global conservation to an inclusive and regenerative conservation. *Environment* **63**, 4–19. (doi:10.1080/00139157.2021.1924574)
15. Madzwamuse M, Rihoy E, Louis M. 2020 Contested conservation: implications for rights, democratization, and citizenship in southern Africa. *Development* **63**, 67–73. (doi:10.1057/s41301-020-00237-1)
16. Dowie M. 2009 *Conservation refugees: the hundred-year conflict between global conservation and native peoples*. Cambridge, MA: The MIT Press.
17. Hare D, Blossey B, Reeve HK. 2018 Value of species and the evolution of conservation ethics. *R. Soc. Open Sci.* **5**, 181038. (doi:10.1098/rsos.181038)
18. Fletcher MS, Hamilton R, Dressler W, Palmer L. 2021 Indigenous knowledge and the shackles of wilderness. *Proc. Natl Acad. Sci. USA* **118**, e2022218118. (doi:10.1073/pnas.2022218118)
19. Peluso NL. 1993 Coercing conservation? The politics of state resource control. *Glob. Environ. Chang.* **3**, 199–217. (doi:10.1016/0959-3780(93)90006-7)
20. Robbins P. 2007 Fortress conservation. In *Encyclopedia of environment and society*, pp. 704–705. Thousand Oaks, CA: SAGE Publications, Inc.
21. Tan KC. 2021 Just conservation: the question of justice in global wildlife conservation. *Phil. Compass* **16**, ePHC312720. (doi:10.1111/phc3.12720)
22. Barber PH *et al*. 2014 Advancing biodiversity research in developing countries: the need for changing paradigms. *Bull. Mar. Sci.* **90**, 187–210. (doi:10.5343/bms.2012.1108)
23. Haelewaters D, Hofmann TA, Romero-Olivares AL. 2021 Ten simple rules for Global North researchers to stop perpetuating helicopter research in the Global South. *PLoS Comput. Biol.* **17**, e1009277. (doi:10.1371/journal.pcbi.1009277)
24. Igoe J, Brockington D. 2020 Neoliberal conservation: a brief introduction. *Conserv. Soc.* **5**, 432–439.
25. Duffy R *et al*. 2019 Why we must question the militarisation of conservation. *Biol. Conserv.* **232**, 66–73. (doi:10.1016/j.biocon.2019.01.013)
26. Lunstrum E. 2014 Green militarization: anti-poaching efforts and the spatial contours of Kruger National Park. *Ann. Assoc. Am. Geogr.* **104**, 816–832. (doi:10.1080/00045608.2014.912545)
27. Oommen MA *et al*. 2019 The fatal flaws of compassionate conservation. *Conserv. Biol.* **33**, 784–787. (doi:10.1111/cobi.13329)
28. Wallach AD, Bekoff M, Batavia C, Nelson MP, Ramp D. 2018 Summoning compassion to address the challenges of conservation. *Conserv. Biol.* **32**, 1255–1265. (doi:10.1111/cobi.13126)
29. Wilson, EO. 2016 *Half-Earth: our planet's fight for life*. London, UK: Liveright Publishing.
30. Büscher B *et al*. 2017 Half-Earth or whole Earth? Radical ideas for conservation, and their implications. *Oryx* **51**, 407–410. (doi:10.1017/S0030605316001228)
31. Shanker K, Oommen MA. 2021 The authoritarian biologist reloaded and deep ecology redux: conservation imperialism and the control of knowledge, money and space. In *A functioning anarchy? Essays for Ramachandra Guha* (eds S Raghavan, N Sundar), pp. 37–54. New Delhi, India: Penguin Random House.
32. Fairhead J, Leach M, Scoones I. 2012 Green grabbing: a new appropriation of nature? *J. Peasant Stud.* **39**, 237–261. (doi:10.1080/03066150.2012.671770)
33. Flores D, Falco G, Roberts NS, Valenzuela FP. 2018 Recreation equity: is the Forest Service serving its diverse publics? *J. For.* **116**, 266–272. (doi:10.1093/jofore/fvx016)
34. Department for Environmental Food and Rural Affairs - UK. 2019 Landscapes review: national parks and AONBs. See https://www.gov.uk/government/publications/designated-landscapes-national-parks-and-aonbs-2018-review (accessed 23 November 2020).
35. Thompson A. 2020 Black birders call out racism, say nature should be for everyone. *Sci. Am.* See https://www.scientificamerican.com/article/black-birders-call-out-racism-say-nature-should-be-for-everyone/ (accessed 17 August 2021).
36. Davis J. 2018 Black faces, black spaces: rethinking African American underrepresentation in wildland spaces and outdoor recreation. *Environ. Plan. E Nat. Sp.* **2**, 89–109. (doi:10.1177/2514848618817480)
37. Buckley R. 2007 Adventure tourism products: price, duration, size, skill, remoteness. *Tour. Manag.* **28**, 1428–1433. (doi:10.1016/J.TOURMAN.2006.12.003)
38. Stodolska M, Shinew KJ, Li MZ. 2010 Recreation participation patterns and physical activity among Latino visitors to three urban outdoor recreation

environments. *J. Park Recreat. Adm.* **28**, 36–56. (doi:10.1080/14927713.2011.615642)

39. Demery AJC, Pipkin MA. 2021 Safe fieldwork strategies for at-risk individuals, their supervisors and institutions. *Nat. Ecol. Evol.* **5**, 5–9. (doi:10.1038/s41559-020-01328-5)
40. Jones B. 2018 For the LGBTQ community, birding can be a relief—and a source of anxiety. *Natl. Audobon Soc.* See https://www.audubon.org/news/for-lgbtq-community-birding-can-be-relief-and-source-anxiety (accessed 17 August 2021).
41. Hunter M. 2007 The persistent problem of colorism: skin tone, status, and inequality. *Sociol. Compass* **1**, 237–254. (doi:10.1111/j.1751-9020.2007.00006.x)
42. Holmes G. 2011 Conservation's friends in high places: neoliberalism, networks, and the transnational conservation elite. *Glob. Environ. Polit.* **11**, 1–21. (doi:10.1162/GLEP_a_00081)
43. O'Brien LT, Bart HL, Garcia DM. 2020 Why are there so few ethnic minorities in ecology and evolutionary biology? Challenges to inclusion and the role of sense of belonging. *Soc. Psychol. Educ.* **23**, 449–477. (doi:10.1007/s11218-019-09538-x)
44. National Science Foundation - National Center for Science and Engineering Statistics. 2019 Women, minorities, and persons with disabilities in science and engineering. Special Report NSF 13-304. See http://www.nsf.gov/statistics/wmpd/. See https://ncses.nsf.gov/pubs/nsf19304/ (accessed 17 August 2021).
45. Fournier AMV, Bond AL. 2015 Volunteer field technicians are bad for wildlife ecology. *Wildl. Soc. Bull.* **39**, 819–821. (doi:10.1002/wsb.603)
46. Morales N, Bisbee O'Connell K, McNulty S, Berkowitz A, Bowser G, Giamellaro M, Miriti MN. 2020 Promoting inclusion in ecological field experiences: examining and overcoming barriers to a professional rite of passage. *Bull. Ecol. Soc. Am.* **101**, e01742. (doi:10.1002/bes2.1742)
47. Hart AG, Leather SR, Sharma MV. 2020 Overseas conservation education and research: the new colonialism? *J. Biol. Educ.* **54**, 1–6. (doi:10.1080/00219266.2020.1739117)
48. Cousins JA, Evans J, Sadler JP. 2009 'I've paid to observe lions, not map roads!'—An emotional journey with conservation volunteers in South Africa. *Geoforum* **40**, 1069–1080. (doi:10.1016/j.geoforum.2009.09.001)
49. Klein M, Weiss F. 2011 Is forcing them worth the effort? Benefits of mandatory internships for graduates from diverse family backgrounds at labour market entry. *Stud. High. Educ.* **36**, 969–987. (doi:10.1080/03075079.2010.487936)
50. Schusler TM, Espedido CB, Rivera BK, Hernandez M, Howerton AM, Sepp K, Engel MD, Marcos J, Chaudhary B. 2020 Students of color speak on racial equity in environmental sustainability. *EcoEvoRxiv* December 1. (doi:10.32942/OSF.IO/NTEZC)
51. UK Research and Innovation. 2020 Diversity results for UKRI funding data. See https://www.ukri.org/wp-content/uploads/2020/10/UKRI-020920-DiversityResultsForUKRIFundingData2014-19.pdf (accessed 23 November 2020).
52. Taylor DE. 2014 The state of diversity in environmental organizations: mainstream NGOs, Foundations & Government Agencies. July, 28–31. See http://orgs.law.harvard.edu/els/files/2014/02/FullReport_Green2.0_FINALReducedSize.pdf.
53. Atherton MC. 2014 Academic preparedness of first-generation college students: different perspectives. *J. Coll. Stud. Dev.* **55**, 824–829. (doi:10.1353/csd.2014.0081)
54. Frieze C, Marculescu D, Quesenberry J, Katilius G, Reynolds J. 2018 'Where are you really from?': mitigating unconscious bias on campus. In *2018 Research on Equity and Sustained Participation in Engineering, Computing, and Technology, RESPECT 2018, 21 February, Baltimore, MD.* Piscataway, NY: IEEE.
55. Sims C, Hirudayaraj M. 2016 The impact of colorism on the career aspirations and career opportunities of women in India. *Adv. Dev. Hum. Resour.* **18**, 38–53. (doi:10.1177/1523422315616339)
56. Wilson JW, Biggs D. 2016 Passport power: entrenching inequality. *Science* **353**, 1216. (doi:10.1126/science.aajl1604)
57. Mcdonald C, Raderschall L. 2019 *Indigenous community capacity and multi-level governance*. Paris: OECD regional development working papers, No. 2019/04. OECD Publishing. (doi:10.1787/8036b14d-en)
58. Hofstra B, Kulkarni VV, Galvez SMN, He B, Jurafsky D, McFarland DA. 2020 The diversity–innovation paradox in science. *Proc. Natl Acad. Sci. USA* **117**, 9284–9291. (doi:10.1073/pnas.1915378117)
59. Brondízio ES *et al*. 2021 Locally based, regionally manifested, and globally relevant: indigenous and local knowledge, values, and practices for nature. *Annu. Rev. Environ. Resour.* **46**, 481–509. (doi:10.1146/annurev-environ-012220-012127)
60. McElwee P *et al*. 2020 Working with indigenous and local knowledge (ILK) in large-scale ecological assessments: reviewing the experience of the IPBES Global Assessment. *J. Appl. Ecol.* **57**, 1666–1676. (doi:10.1111/1365-2664.13705)
61. Cech EA, Metz A, Smith JL, deVries K. 2017 Epistemological dominance and social inequality: experiences of Native American science, engineering, and health students. *Sci. Technol. Hum. Values* **42**, 743–774. (doi:10.1177/0162243916687037)
62. Kimmerer RW. 2021 *Braiding sweetgrass*. Minneapolis, MN: Milkweed Editions.
63. Cajete G, Bear LL. 2000 *Native science: natural laws of interdependence*. Santa Fe, NM: Clear Light Publishers.
64. Race AI, Beltran RS, Zavaleta ES. 2021 How an early, inclusive field course can build persistence in ecology and evolutionary biology. *Integr. Comp. Biol.* **61**, 957–968. (doi:10.1093/icb/icab121)
65. Cheng SJ, Mourad T, Goldberg DE, Middendorf G, Prevost LB, McKay TA. 2021 Harnessing data for inclusive ecology education: building programs to move the discipline toward systemic change. *Bull. Ecol. Soc. Am.* **102**, e01842. (doi:10.1002/bes2.1842)
66. Sheffield SL, Cook ML, Ricchezza VJ, Rocabado GA, Akiwumi FA. 2021 Perceptions of scientists held by US students can be broadened through inclusive classroom interventions. *Commun. Earth Environ.* **2**, 83. (doi:10.1038/s43247-021-00156-0)
67. Arif S *et al*. 2021 Ten simple rules for supporting historically underrepresented students in science. *PLoS Comput. Biol.* **17**, e1009313. (doi:10.1371/journal.pcbi.1009313)
68. PLOS One. 2021 Inclusivity in global research. Best practices in research reporting. See https://journals.plos.org/plosone/s/best-practices-in-research-reporting#loc-inclusivity-in-global-research (accessed 5 October 2021).
69. Athayde S, Silva-Lugo J, Schmink M, Kaiabi A, Heckenberger M. 2017 Reconnecting art and science for sustainability: learning from indigenous knowledge through participatory action-research in the Amazon. *Ecol. Soc.* **22**. (doi:10.5751/ES-09323-220236)
70. Milich KM, Sorbello K, Kolinski L, Busobozi R, Kugonza M. 2021 Case study of participatory action research for wildlife conservation. *Conserv. Sci. Pract.* **3**, e347. (doi:10.1111/csp2.347)
71. Wedemeyer-Strombel KR *et al*. 2019 Engaging fishers' ecological knowledge for endangered species conservation: four advantages to emphasizing voice in participatory action research. *Front. Commun.* **4**, 30. (doi:10.3389/fcomm.2019.00030)
72. Galvin KA, Beeton TA, Luizza MW. 2018 African community-based conservation: a systematic review of social and ecological outcomes. *Ecol. Soc.* **23**, 29. (doi:10.5751/ES-10217-230339)
73. Rivera Lopez F, Wickson F, Hausner VH. 2018 Finding CreativeVoice: applying arts-based research in the context of biodiversity conservation. *Sustainability* **10**, 1778. (doi:10.3390/su10061778)
74. Andrachuk M, Marschke M, Hings C, Armitage D. 2019 Smartphone technologies supporting community-based environmental monitoring and implementation: a systematic scoping review. *Biol. Conserv.* **237**, 430–442. (doi:10.1016/j.biocon.2019.07.026)
75. Johnson JT, Howitt R, Cajete G, Berkes F, Louis RP, Kliskey A. 2016 Weaving indigenous and sustainability sciences to diversify our methods. *Sustain. Sci.* **11**, 1–11. (doi:10.1007/s11625-015-0349-x)
76. Valenzuela-Toro AM, Viglino M. 2021 How Latin American researchers suffer in science. *Nature* **598**, 374–375. (doi:10.1038/D41586-021-02601-8)
77. Massey MDB, Arif S, Albury C, Cluney VA. 2021 Ecology and evolutionary biology must elevate BIPOC scholars. *Ecol. Lett.* **24**, 913–919. (doi:10.1111/ELE.13716)
78. Gewin V. 2021 How to include Indigenous researchers and their knowledge. *Nature* **589**, 315–317. (doi:10.1038/D41586-021-00022-1)

# 6. Discussion

Central to this thesis is an exploration of African lion conservation through an interdisciplinary lens, combining behavioural ecology and social science methods. This approach facilitates the examination of a multifaceted conservation problem across various scales. First, the social behaviour of individual lions across their lifetime, and inter-individual association patterns, have been understudied to date. This thesis presents novel evidence of sex-modulated social ageing in the species, adding to a growing field of literature on age-structured societies. In addition, I show that losing associates impacts individuals' sociality, and that females demonstrate stark changes in their social association patterns prior to disappearing from the system. Combined these findings have varied ecological implications with relevance to the species' conservation, particularly regarding the management of disease. Second, I demonstrate the role that bias against lion conservation messengers can have on their perception in the public eye, and in turn, public support for their management recommendations. Specifically, I evidence racism and sexism in keeping with broader societal discrimination. I then outline why such injustice is particularly concerning against the backdrop of conservations colonial history, before providing recommendations to overcome these systems of oppression.

In this chapter I summarise the contributions this thesis makes to knowledge through the work presented in **Chapters 2-5**, before discussing its limitations and suggesting the most pressing gaps that remain to be addressed.

## 6.1. Summaries and contextualisation of key results

In **Chapter 2**, I examined patterns of social ageing, and social predictors of longevity, in the wild Serengeti lion population. I created spatially explicit annual social networks using 30 years of observational data to generate a suite of individual-level social metrics. Testing these metrics across individuals' lifetimes produced evidence of strong divergence in the way sex modulates social ageing and longevity in this population. Both females and males were found in increasingly large sub-groups as they aged. However, only males demonstrated changes in the number of associates they had, and specifically the number of female associates they had, which peaked in mid-life before declining. The same mid-life peak existed for males' connectivity strength to females. Conversely, an early- and late-life peak was evident in males' connectivity strength and bondedness to other males. Females showed significant declines in their connectivity strength and bondedness to other females as they aged. In addition, they peaked in connectivity and bondedness to males in mid-life. While female longevity increased with greater overall connectivity and lower cliquishness amongst their associates, male longevity was predicted by the number of associates they had. This suggest that the quantity of social associations has a bigger impact on survival in male lions than females, who are instead affected by the quality of their associations. There may be a range of ecological and conservation implications of these results for age-structured lion societies due to the role of sociality in processes such as social learning and disease spread.

In **Chapter 3** I sought to build on these findings by illuminating the drivers of the identified social ageing patterns. I focused on two hypotheses with contextual relevance to both the natural demography and conservation threats of the Serengeti lion population: within-individual social behaviour shifts prior to disappearance from the population, and the impact of associate loss on the sociality of remaining individuals. Using the same data, method of social network construction, and metrics generated (minus clustering) as in **Chapter 2**, I first investigated whether individual-level sociality differed in the year prior to, and the year of, an individuals' disappearance from the population. Next, I tested whether individuals' social response to losing an associate was dependent on their connectivity strength to that lost individual in the previous year. Once again, sex strongly modulated the observed patterns. Declines in the quality and quantity of lionesses' social associations were evident prior to their disappearance from the population, although they were found in larger sub-groups. There were also evident declines in female intra-sex connectivity strength and bondedness after they lost female associates, while losing male associates resulted in declines in female sub-group size. The effects of associate loss and pre-disappearance sociality shifts were less evident in males. However, they were found in smaller sub-groups and with fewer females after losing male associates but were more closely bonded to their female associates.

In **Chapter 3**, with pre-disappearance and post-associate loss sociality effects accounted for in the models, most of the female social ageing and longevity effects detected in **Chapter 2** were lost (apart from senescent declines in intra-sex bond strength). This suggests a strong role of both within-individual changes and population-level changes on declines in lionesses' social connectivity with age. The ageing and longevity effects outlined in **Chapter 2** remained significant for males, which indicates an alternative driver (i.e., not individual pre-disappearance changes or associate loss) of these patterns. It may simply be that ageing males exist in larger and larger prides as they continue to father cubs, many of which remain within the natal pride. This could explain the detected increases in sub-group size and number of unique female associates. The decline in intra-sex connectivity may result from the increasing probability of losing coalition-mates over time, as they are rarely replaced by new males[1]. The lack of persistence of longevity effects for both sexes does indicate an absence of selective disappearance in this population[2]. This was to be expected, given knowledge of factors outside of individual social behaviour that will have significant impacts on individual survival odds (e.g., pride size, territory quality, and hunting success[1,3–5]).

Combined, **Chapters 2 and 3** provide novel insights into social ageing in a fission-fusion carnivore society. Our knowledge of the diagnostics of social ageing in wild populations is still in its infancy, and even less understood are the consequences of social ageing[2,6–9]. Through these research chapters I highlight potential answers to each of these questions. The uncovering of sex-specific patterns is important for understanding both age-structured lion societies, and more broadly, the ecological and evolutionary implications of social ageing across species[6]. My findings suggest plausible consequences of social ageing for wild lions, particularly regarding social learning[10–13] and pathogen exposure[14–16]. The latter is likely to be of specific interest in the context of lion conservation given the cyclical resurgence of lethal diseases such as CDV in the

Serengeti lion population[17,18]. As this population is considered one of the few remaining stable lion populations[19], its persistence is crucial for the enduring success of the species.

Considering the conservation relevance of the results produced in **Chapters 2 and 3**, I was interested in understanding factors that might influence human perceptions of scientific information, especially as it relates to policy and decision-making in lion conservation. Therefore, in **Chapter 4,** I looked more broadly at behaviour in the lion conservation community, and specifically at factors influencing public opinion of conservation messengers and the lion management strategies they communicate. I hypothesised that the identity of a conservation messenger would bias public perceptions of their management recommendations when communicating on X (formerly Twitter). Using an online vignette-style experiment, and data from 1290 participants based in the UK, I tested whether a messenger's gender, race, nationality and expertise impacted several variables. These were i) the perceived credibility of their lion conservation recommendation, ii) support for implementing that recommendation, and iii) the perceived trustworthiness of the messenger. I found that while men were perceived to be more credible than women, it was the interaction between the messenger's race and expertise that influenced support for implementing the strategy and explicit trust in the messenger. White professors' lion conservation recommendations were more strongly supported than those of Black professors, and the same was true of their respective trustworthiness. In addition, explicit trust depended on the interaction between race and gender, with Black women the least trusted. Public opinion in conservation is highly important, as it has the power to sway politicians and conservation organisations through the direction of funds and support[20–23]. While unsurprising, finding the identity of conservation messengers could influence the weight their voices carry in management debates has important implications. The prevalence of discrimination in conservation could be particularly harmful considering the ongoing injustices that are rife within the sector[24].

Reflecting on this, I widened the lens to examine past and present behaviour in the conservation community more generally, as a means of providing broader suggestions for altering behaviour to address these identity-based inequities. In **Chapter 5,** I highlight the ways in which racism and systemic oppression continue to be upheld in conservation because of the reinforcing cycles that exist between science and practice. I argue that conservations' colonial roots impact academic conceptualisations of conservation problems and research priorities, how conservation is taught, and approaches to collaboration (or lack thereof) with local communities. As such, graduates carry biases that they apply in their future work, whether within the policy, NGO, corporate, or academic spheres of conservation. This in turn influences decision-making in conservation practice, impacting definitions of success which lack consideration of human rights and wellbeing, in favour of nature and biodiversity-focused outcomes. As such, and in collaboration with a global, diverse, and interdisciplinary team of experts, I produced a suite of recommendations to guide researchers, practitioners and institutions towards more equitable and anti-racist methods of working. These were centred around three concepts; i) recognising and addressing the unjust history of conservation, ii) constructing more equitable ways of conducting research and practice, and iii) fostering an inclusive, safe, conservation space that allows BIPOC individuals to thrive.

Until the conservation community collectively prioritises these foundational steps towards addressing injustice, we will continue to perpetuate longstanding cycles of oppression. This will be reflected in conservation science through a lack of retention of marginalised individuals as they are excluded by unsupportive work environments, which will in turn limit the diversity of perspectives in the field[25]. Despite the progress that has been made in recent years, what we still lack is committed action from those in the conservation science community with the most power. Currently, the burden of advocacy against racism and neo-colonial attitudes is carried by those most vulnerable in terms of job security and (workplace, in the broadest sense) social exclusion. While conservation scientists who are BIPOC and those who are otherwise marginalised/multiply marginalised should instruct on the reform of conservation science, those in power must actively lend their support. This could come in the form of speaking out against bad practice within their workplaces, encouraging colleagues to reflect on the implications of their work, or vocally advocating for the rights of those marginalised by conservation. Given the power of representation, it will also be important that the conservation community publicly acknowledge the conservation expertise held by Indigenous people, local communities, and scholars of colour[26]. If not, conservation scientists will continue to facilitate the oppression of some of the world’s most vulnerable communities at the expense of conservation outcomes[24,27], with such dynamics exacerbated by the disproportionate effects of the ongoing climate crisis[28].

## 6.2. Limitations and future directions

The limitations of the work presented in this thesis are examined separately and in detail within the discussions of the specific research chapter in question (**Chapters 2-5)**. However, in this section I will contextualise the data used, address its limitations in addressing the aims of the thesis, and propose fruitful research avenues for future work based on my findings.

### 6.2.1. The Serengeti lion data and social ageing knowledge gaps

The results presented in **Chapters 2 and 3** are based on the analysis of data collected by the Serengeti Lion Project. The data were never collected with the social network analyses I conducted in mind, meaning there were several ways in which it was non-optimal for this purpose. This is often true across long-term study populations, with data collected for one purpose and later adapted for novel research as new areas emerge. Though the Serengeti Lion Project ran from the 1960s to 2014, I only used data collected after the start of their GPS collaring program which began in 1984. Within this dataset, it is worth noting that most collared individuals were females, so there is relatively less data available for males. Even less data is available for males that were not actively resident within a pride, and fewer males lived to old age. Therefore, targeted efforts to collar males and collect data regarding their sociality during and post-pride residency would markedly improve knowledge of the drivers of male social ageing. An unexplored area of particular interest is whether signs of physical deterioration correlate with males spending more of their time with the females (and cubs) in their prides. Whether due to explicit recognition of their vulnerability to intruders, or declining energy and so dependence on the pride, evidence of such patterns (or lack thereof) would help illuminate the drivers of social ageing in males.

It will also be important to consider signs of physical and cognitive senescence alongside increasing age in both sexes. This combination of data is missing in studies of social ageing in wild populations to date, and instead researchers correlate age with broad senescence. We know that physical and cognitive senescence in humans do not uniformly progress in severity and pace across individuals[29,30], so it is plausible the same is true of other species. As such, this combined approach remains an understudied and likely rich area for future research across species and systems. In lions, whether the onset of changes in individuals' social behaviour align with signs of physical ageing such as tooth wear or reductions in body mass could help to explain between-individual variation in social ageing. In addition, recent studies of cognitive function in captive lions have provided evidence of individual variation in cognitive ability, in both cooperative and solitary tasks[31–33]. Examining whether senescent declines in cognition exist, and whether these align with shifts in individual sociality, could further illuminate drivers of social ageing in the species.

Throughout the analyses in **Chapters 2 and 3**, spatial autocorrelation in social network metrics was evident. Though not the specific focus of my research, future studies should consider why sociality is spatially arranged in this system, and in which ways. The Serengeti landscape is highly heterogenous, particularly across the seasons[34,35]. Given the importance of environmental features such as river confluences on lion fitness[4], it is likely that such heterogeneity will further influence individual-sociality. Whether lions vary their social behaviour and associate-interaction patterns in different areas of their territory, and whether ageing individuals alter their spatial behaviour thereby impacting their sociality, remains to be understood.

In **Chapter 3** I considered including the age of the lost individual in the models as a predictor of the remaining individual's social response. Unfortunately, low data availability in the spread of ages at which individuals were lost created issues with model convergence. In future work, an alternative could be to simulate the effects of the loss of individuals of different ages, using a model parametrised with this data. A modelling approach could also facilitate similar research across smaller and more data deficient lion populations. Such modelling approaches have been successfully implemented to investigate similar dynamics in other species[36,37]. Additional characteristics could also be worth investigating, such as the network centrality of the individual prior to their disappearance[38]. In this way, it would be possible to examine the impact of losing specific individuals from the population on phenomena such as disease spread and information transfer. Not only will such examinations aid our understanding of the drivers of social ageing in lions - thereby illuminating the underlying evolutionary and ecological mechanisms - they will also be crucial to species conservation efforts.

Although the African lion is listed as vulnerable by the IUCN[19], the Serengeti population is one of the largest, most stable, and well-studied across generations. The fact that a considerable proportion of individuals in this population survive to “old age” may be unique. While this is beneficial in terms of data availability (with a large sample size), findings from this population may therefore be limited in their applicability to smaller systems. Studying social ageing in smaller populations, or those that face greater anthropogenic pressures, is now of great interest. That said, there are significant threats to the long-term stability of the Serengeti population, and of most relevance to the work in **Chapters 2 and 3** of this thesis is disease risk.

It was my initial intent to investigate changes to the sociality of the Serengeti lion population during and post disease outbreaks. The Serengeti lion population has experienced several disease outbreaks in recent years, but most notable is the CDV outbreak of 1994, which caused the death of a third of the population[18]. The higher-than-expected lethality of the disease (based on previous, less severe outbreaks) was driven by drought conditions in the year prior, which caused an uptick in the prevalence of *Babesia* parasites in Cape buffalo (*Syncerus caffer*), a major prey source for Serengeti lions[1]. Co-infection with *Babesia* and CDV drove lion mortality[17]. Indeed, reductions in the overall social connectivity of the population, particularly between prides, are evident from initial mapping of the networks (Figure 1).

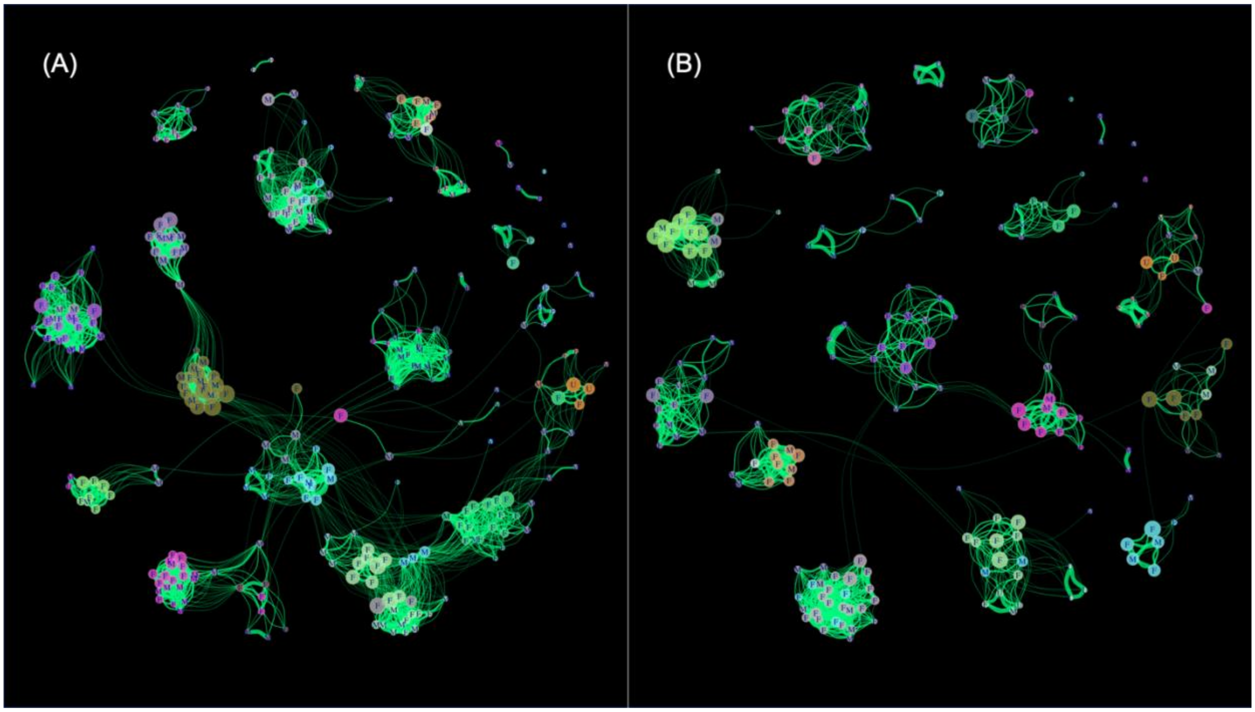

**Figure 1. Population-level social networks for the seasonal year (A) 1993 and (B) 1994.** Social networks for the year prior to, and year of, the high-lethality CDV outbreak in the Serengeti lion population. Nodes denote individuals, edges denote associations derived from co-observation on the same date at the same GPS points (following the methodology outlined in chapters 1 and 2). Letters denote sex, F = female, M = male, U = unknown.

Despite an obvious visual reduction, such effects were difficult to detect using similar network modelling techniques as employed in **Chapters 2 and 3**. With networks generated at yearly intervals it was difficult to identify any disease-induced individual-level changes in behaviour. This was especially true in the absence of population wide data on individual positivity for CDV. Generating networks at shorter time intervals was not a reliable option due to the observation frequencies of individuals. The results of **Chapter 3** indicate variation in the response of individuals to associate loss, dependent on the characteristics of both the individual lost and the individual remaining, and notable shifts in sociality prior to disappearing from the population in females. Our knowledge of whether such dynamics persist during periods of high turnover, such as disease outbreaks, is limited. Understanding the influence of high-mortality periods on the social landscape will be important in curbing the spread, and therefore lethality, of future disease outbreaks. To address such questions, and as suggested earlier in the discussion, it may instead be more productive to parametrise a model and simulate social dynamics during and after historic CDV outbreaks.

### 6.2.2. Limitations of behavioural ecology for lion conservation

What the data used in **Chapters 2 and 3** of this thesis cannot account for are the impacts of people on lions, and vice versa. I list this as a limitation of both the data and in addressing the overall thesis aim (improving our holistic knowledge of lion behaviour and conservation to improve species management), because of the history of the Serengeti landscape, which is clouded with human-rights abuses committed in the name of conservation[39]. While giving a full and comprehensive account of that history is outside of the scope of this thesis, I will provide a brief overview to contextualise the data and the system within which it sits. The Serengeti was initially designated a game reserve under the German occupation of Tanzania, before being gazetted as a National Park in the 1950s by the British during their colonial regime[39]. Both cases saw increasing restrictions on land use within the boundaries by IPLCs who were violently and forcibly removed, while land was protected for the use and enjoyment of European colonists[40]. The largest community inhabiting the region at the time were the Maasai, (but several other communities were resident), who were either forced to resettle around the outskirts of the unfenced park or were relocated to the neighbouring Ngorongoro district[41]. Today the Maasai continue to face mass evictions from this district, with human-rights violations regularly reported including the use of military force, arrests, and mass burning of homes[42,43]. Such actions aim to remove Maasai people from the land so that it can also be assigned a protected conservation status. This would facilitate use of the land by wealthy (predominantly foreign) actors for leisure, but restrict access for local communities, echoing the situation in the Serengeti landscape over 50 years ago.

While lion conservation can be aided by improving to our knowledge of behavioural ecology as I have done in **Chapters 2 and 3**, the future of the species depends on our ability to reach, and fund, equitable land management solutions. As discussed in **Chapter 5**, conservation that continues to facilitate neo-colonial practices (such as land grabbing) at the expense of human rights will not succeed[27,44]. Such practices are not only unjust but impractical given the continual growth and development of human populations across lion range countries. In addition, conservation management strategies that contradict the will of local people have been evidenced to be less successful[45]. The impact of human-lion conflict along the borders of the Serengeti National Park is increasingly well studied, with lions posing a real threat to the lives and livelihoods of local people, which incites retaliation[46,47]. What is less understood is the impact of tourism and the prioritisation of distant elites' desires regarding conservation management strategies on local peoples' attitudes towards lions. Further, we lack knowledge of the impacts of tourism inside the park on lion populations- including the effects vehicles and infrastructure on the behaviour of lions and their prey, habitat degradation, and pollution (including the climate impacts of global travel). Such factors in areas of high tourist abundance have been shown to reduce cub recruitment in the cheetah (*Acinonyx jubatus*) population of the Maasai Mara National Reserve in Kenya[48], which borders the Serengeti National Park.

Vast amounts of money are required to conserve wild lions[49], and it is undeniable that tourism is a major contributor to that. However, the ethics of continuing to perpetuate historic cycles of injustice in the name of conservation are increasingly under scrutiny[50,51]. As discussed in **Chapter 4**, dismantling our (as a global societies) perception biases of the most pertinent risks to wildlife, whose wellbeing should be prioritised, and whose opinion of management strategies is heard, will be key to conserving species such as the African lion. Doing so will require traditionally trained conservation scientists to not only expand their research approaches to include social science methodologies, but actively engage colleagues in disciplines such as political ecology, geography, psychology and history.

### 6.2.3. Future avenues for a holistic view of lion conservation

The results presented in **Chapter 4** used data that were purposefully collected to address the aims of the research. As such, there were significantly fewer limitations of the data itself comparative to the data used in **Chapters 2 and 3**. Despite this there are still several limitations which should be noted, alongside discussing some of the key questions for future work to consider.

I intentionally chose not to situate the example of lion conservation given in the “X profiles” in the Serengeti, or any specific geographic area. As already discussed, Serengeti National Park is an iconic, well-known conservation area. It is reasonable to assume that most people in the UK have at least heard of it (if not visited it or watched documentaries about it) which means they are likely to carry preconceptions about issues related to lion conservation in the park. I was further concerned that such background knowledge might extend beyond Serengeti National Park to other systems in Tanzania and neighbouring Kenyan national parks. The same was likely to be true of lion conservation in South Africa, given the equally famous national parks such as Kruger. For this reason, I chose to leave the location of the outlined lion conservation scenario ambiguous. The choice to compare the UK and Zimbabwe in terms of the messenger’s location/nationality followed similar logic. Zimbabwe is a lion range country that receives little media attention for conservation-related topics in the UK. In addition, I was working with a Zimbabwean co-author, providing the situational expertise necessary to ensure the profiles were believable - with my own nationality providing the same situational expertise for the UK based messengers.

As discussed extensively in **Chapter 4**, I was interested in understanding how the identity of the messengers impacted public perceptions, and as such it was vital to hold the posted lion conservation message constant. With the results of this chapter in mind, it would now be interesting to run a similar study to investigate the effect of varying the message itself. The preliminary study conducted to select the lion conservation strategy for use in the main study showed strong public disagreement with the idea of permitting trophy hunting to conserve habitat for lions, and strong agreement with the idea of banning trophy hunting to protect lions. Embedding these different strategies in posts within the profiles of conservation messengers we know generate low versus high public trust (e.g., a Black professor and a white professor) would allow us to understand whether the controversial nature of certain conservation strategies is enough to sway public opinion of a conservation messenger.

Manipulating factors other than the messenger's identity may also be of value. For example, repeating the study and manipulating factors such as the presence of a blue tick, and the number of followers, would demonstrate the role of societal perceptions of expertise on individual opinion. In addition, research has shown that the perceived charisma and worth of species is vastly different between publics in countries they inhabit and foreign publics[52]. As such, testing publics outside of the UK, and especially in countries with wild lion populations, would provide a comparative element. Testing the perceptions of people within the conservation community, such as policy makers and funding bodies, might further illuminate the role bias plays in conservation prioritisation outside of the public realm. Finally, considerable work has shown the effect that accents can have in generating a sense of in-group belonging and trust in the information being conveyed[53–55]. Understanding whether such audio-based biases have an impact on perceptions of conservation messengers, especially regarding media such as TV documentaries and news interviews, is now of great interest.

The results of **Chapter 4** raise interesting ethical considerations in relation to conservation message framing, which is receiving increasing research attention[56–58]. Predominantly the focus of such research is on how to leverage public biases to enact behaviour change, or garner support for specific conservation strategies[59–62]. Additional work has prescribed methods for designing the most effective celebrity endorsed conservation-behaviour interventions[63], which advocates for leveraging such qualities as the “attractiveness” and “perceived expertise” of the messenger. Across these spheres of research is a lack of critical engagement with literature on identity-bias in relation to such qualities[64–66], and even less critical engagement with conservations’ colonial history and enduring social injustices. The absence of such critical thought and apparent willingness to cater to societal biases will perpetuate the continual fuelling of unjust systems in conservation. Instead, the work presented in this thesis advocates for dismantling such systems, which first and foremost requires acknowledging that they exist, and platforming those whose expertise should be valued even if they would not traditionally be perceived as experts.

**Chapter 5** was perspective driven, and as such there are no direct data limitations. However, there are several limitations in its scope, and since it was written a growing body of work has been published on related topics. Many of these manuscripts have focused on the need to decolonise ecology and conservation[67,68], and centre equity, justice, and inclusion[69–73] in our approaches. A great deal of attention has also been paid to topics only briefly discussed in **Chapter 5** - reducing sexuality, gender identity, ableism, language and geography related access barriers[74–83]; and with specific attention paid to the difficulties that fieldwork can pose[84–86]. Where I continue to see gaps are, as expressed throughout this discussion, in the conservation community's willingness to reflect on the ways our conceptualisation of conservation action continues to feed systems of oppression and prioritise the needs of the (globally) privileged. Often, this is done at the expense of positioning local communities as the conservation problem, without critically and quantitatively examining the negative effects of foreign influence (both past and present) on conservation outcomes. This prioritisation further expands to the desires of researchers and practitioners to travel to and work in designated conservation spaces, without engaging in the colonial history of the land[87]. While this happens with the intention of improving conservation outcomes, we must commit to reflecting on the ethics of imposing external perspectives at the expense of respecting the rights of local communities to manage their land and the wildlife within it.

Colonially derived methods of conservation are inherently flawed and were devised with a power-first mentality. Over the past 50 years, conservation knowledge production related to wildlife and landscapes in the Global South has been dominated by researchers from the Global North[44]. Increasingly, the leadership that Indigenous people and local communities will have in protecting our natural resources and ecosystems is being recognised by the conservation community[88–90]. We must treat traditional ecological knowledge and Indigenous knowledge systems with respect if we are to successfully tackle the mounting challenges of wildlife conservation in a changing world. Further, recognising the value of being proactive in speaking out against ongoing environmental destruction and land-grabbing at the expense of the lives and wellbeing of Indigenous people and local communities cannot be understated if the conservation community is truly committed to preventing ongoing cycles of oppression and injustice.

## 6.4. Concluding remarks

Historic approaches to lion conservation were rooted in behavioural ecology, leading to a deep understanding of the species through this lens. Recent years have seen substantial shifts towards examining the human dimensions of lion conservation. This thesis contributes to both approaches, by addressing important knowledge gaps within the complex system of lion conservation. Using novel analytical methods, I contribute insights into lion social ageing, which was previously unstudied and has multifaceted relevance to species conservation management. In addition, I contribute knowledge of biases in lion conservation, particularly regarding public perceptions of conservation messengers on social media. By positioning this within the colonial history of lion conservation, I produce recommendations for overcoming discrimination, which will aid in creating a more socially just and effective system of conservation.

## 6.5. References

1. Packer, C. (2023). The Lion: Behvaiour, ecology and conservation of an iconic species (Princeton University Press).

2. Albery, G.F., Clutton-Brock, T.H., Morris, A., Morris, S., Pemberton, J.M., Nussey, D.H., and Firth, J.A. (2022). Ageing red deer alter their spatial behaviour and become less social. Nat. Ecol. Evol. *6*, 1231–1238. https://doi.org/10.1038/s41559-022-01817-9.

3. VanderWaal, K.L., Mosser, A., and Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Anim. Behav. *77*, 949–954. https://doi.org/10.1016/j.anbehav.2008.12.028.

4. Mosser, A., Fryxell, J.M., Eberly, L., and Packer, C. (2009). Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. Ecol. Lett. *12*, 1050–1060. https://doi.org/10.1111/j.1461-0248.2009.01359.x.

5. Scheel, D., and Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. Anim. Behav. *41*, 697–709. https://doi.org/10.1016/S0003-3472(05)80907-8.

6. Woodman, J., Gokcekus, S., Beck, K., Green, J., Nussey, D., and Firth, J. (2024). The ecology of ageing in wild societies: linking age structure and social behaviour in natural populations (Life Sciences) https://doi.org/10.32942/X21893.

7. Siracusa, E.R., Higham, J.P., Snyder-Mackler, N., and Brent, L.J.N. (2022). Social ageing: exploring the drivers of late-life changes in social behaviour in mammals. Biol. Lett. *18*, 20210643. https://doi.org/10.1098/rsbl.2021.0643.

8. Machanda, Z.P., and Rosati, A.G. (2020). Shifting sociality during primate ageing. Philos. Trans. R. Soc. B Biol. Sci. *375*, 20190620. https://doi.org/10.1098/rstb.2019.0620.

9. Rosati, A.G., Hagberg, L., Enigk, D.K., Otali, E., Emery Thompson, M., Muller, M.N., Wrangham, R.W., and Machanda, Z.P. (2020). Social selectivity in aging wild chimpanzees. Science *370*, 473–476. https://doi.org/10.1126/science.aaz9129.

10. McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J., and Moss, C. (2011). Leadership in elephants: the adaptive value of age. Proc. R. Soc. B Biol. Sci. *278*, 3270–3276. https://doi.org/10.1098/rspb.2011.0168.

11. Chiyo, P.I., Moss, C.J., and Alberts, S.C. (2012). The influence of life history milestones and association networks on crop-raiding behavior in male african elephants. PLoS ONE *7*. https://doi.org/10.1371/journal.pone.0031382.

12. Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. Proc. R. Soc. B Biol. Sci. *279*, 4199–4205. https://doi.org/10.1098/rspb.2012.1591.

13. Boogert, N.J., Nightingale, G.F., Hoppitt, W., and Laland, K.N. (2014). Perching but not foraging networks predict the spread of novel foraging skills in starlings. Behav. Processes *109*, 135–144. https://doi.org/10.1016/j.beproc.2014.08.016.

14. Silk, M.J., Croft, D.P., Delahay, R.J., Hodgson, D.J., Boots, M., Weber, N., and McDONALD, R.A. (2017). Using social network measures in wildlife disease ecology, epidemiology, and management. BioScience *67*, 245–257. https://doi.org/10.1093/biosci/biw175.

15. Albery, G.F., Sweeny, A.R., and Webber, Q. (2023). How behavioural ageing affects infectious disease. Neurosci. Biobehav. Rev. *155*, 105426. https://doi.org/10.1016/j.neubiorev.2023.105426.

16. Siracusa, E.R., Pavez-Fox, M.A., Negron-Del Valle, J.E., Phillips, D., Platt, M.L., Snyder-Mackler, N., Higham, J.P., Brent, L.J.N., and Silk, M.J. (2024). Social ageing can protect against infectious disease in a group-living primate. Preprint, https://doi.org/10.1101/2024.03.09.584237 https://doi.org/10.1101/2024.03.09.584237.

17. Munson, L., Terio, K.A., Kock, R., Mlengeya, T., Roelke, M.E., Dubovi, E., Summers, B., Sinclair, A.R.E., and Packer, C. (2008). Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. PLoS ONE *3*, 5–10. https://doi.org/10.1371/journal.pone.0002545.

18. Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofman-Lehmann, R., Lutz, H., et al. (1996). A canine distemper virus epidemic in Serengeti lions (Panthera leo). Nature *379*, 441–445. https://doi.org/10.1038/379441a0.

19. Nicholson, S.K., Bauer, H., Strampelli, P., Sogbohossou, E., Ikanda, D., Tumenta, P.F., Venktramen, M., Chapron, G., and Loveridge, A. (2023). Panthera leo. IUCN Red List Threat. Species *e.T15951A231696234*.

20. Anderson, B., Böhmelt, T., and Ward, H. (2017). Public opinion and environmental policy output: a cross-national analysis of energy policies in Europe. Environ. Res. Lett. *12*, 114011. https://doi.org/10.1088/1748-9326/aa8f80.

21. Larson, L.R., Stedman, R.C., Cooper, C.B., and Decker, D.J. (2015). Understanding the multi-dimensional structure of pro-environmental behavior. J. Environ. Psychol. *43*, 112–124. https://doi.org/10.1016/j.jenvp.2015.06.004.

22. Martín-López, B., Montes, C., Ramírez, L., and Benayas, J. (2009). What drives policy decision-making related to species conservation? Biol. Conserv. *142*, 1370–1380. https://doi.org/10.1016/j.biocon.2009.01.030.

23. Hare, D., Dickman, A.J., Johnson, P.J., Rono, B.J., Mutinhima, Y., Sutherland, C., Kulunge, S., Sibanda, L., Mandoloma, L., and Kimaili, D. (2024). Public perceptions of trophy hunting are pragmatic, not dogmatic. Proc. R. Soc. B Biol. Sci. *291*, 20231638. https://doi.org/10.1098/rspb.2023.1638.

24. Chaudhury, A., and Colla, S. (2020). Next steps in dismantling discrimination: Lessons from ecology and conservation science. Conserv. Lett., e12774. https://doi.org/10.1111/conl.12774.

25. Hofstra, B., Kulkarni, V.V., Galvez, S.M.N., He, B., Jurafsky, D., and McFarland, D.A. (2020). The diversity–innovation paradox in science. Proc. Natl. Acad. Sci. U. S. A. *117*, 9284–9291. https://doi.org/10.1073/pnas.1915378117.

26. Gewin, V. (2021). How to include Indigenous researchers and their knowledge. Nature *589*, 315–317. https://doi.org/10.1038.

27. Domínguez, L., and Luoma, C. (2020). Decolonising conservation policy: How colonial land and conservation ideologies persist and perpetuate indigenous injustices at the expense of the environment. Land *9*, 11–14. https://doi.org/10.3390/land9030065.

28. Ogunbode, C.A. (2022). Climate justice is social justice in the Global South. Nat. Hum. Behav. *6*, 1443–1443. https://doi.org/10.1038/s41562-022-01456-x.

29. Melzer, D., Pilling, L.C., and Ferrucci, L. (2020). The genetics of human ageing. Nat. Rev. Genet. *21*, 88–101. https://doi.org/10.1038/s41576-019-0183-6.

30. Vaupel, J.W. (2010). Biodemography of human ageing. Nature *464*, 536–542. https://doi.org/10.1038/nature08984.

31. Borrego, N. (2020). Socially tolerant lions (Panthera leo) solve a novel cooperative problem. Anim. Cogn. *23*, 327–336. https://doi.org/10.1007/s10071-019-01336-4.

32. Borrego, N., and Dowling, B. (2016). Lions (Panthera leo) solve, learn, and remember a novel resource acquisition problem. Anim. Cogn. *19*, 1019–1025. https://doi.org/10.1007/s10071-016-1009-y.

33. O’Connor, V.L., Thomas, P., Chodorow, M., and Borrego, N. (2022). Exploring innovative problem-solving in African lions (Panthera leo) and snow leopards (Panthera uncia). Behav. Processes *199*, 104648. https://doi.org/10.1016/j.beproc.2022.104648.

34. Reed, D.N., Anderson, T.M., Dempewolf, J., Metzger, K., and Serneels, S. (2009). The spatial distribution of vegetation types in the Serengeti ecosystem: the influence of rainfall and topographic relief on vegetation patch characteristics. J. Biogeogr. *36*, 770–782. https://doi.org/10.1111/j.1365-2699.2008.02017.x.

35. Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., and Sinclair, A.R.E. (2005). Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. Most, 390–393.

36. Williams, R., and Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. Biol. Lett. *2*, 497–500. https://doi.org/10.1098/rsbl.2006.0510.

37. Manno, T.G. (2008). Social networking in the Columbian ground squirrel, Spermophilus columbianus. Anim. Behav. *75*, 1221–1228. https://doi.org/10.1016/j.anbehav.2007.09.025.

38. Firth, J.A., Voelkl, B., Crates, R.A., Aplin, L.M., Biro, D., Croft, D.P., and Sheldon, B.C. (2017). Wild birds respond to flockmate loss by increasing their social network associations to others. Proc. R. Soc. B Biol. Sci. *284*. https://doi.org/10.1098/rspb.2017.0299.

39. Neumann, R.P. (1995). Ways of Seeing Africa: Colonial Recasting of African Society and Landscape in Serengeti National Park. Ecumene *2*, 149–169. https://doi.org/10.1177/147447409500200203.

40. Kideghesho, J.R. (2008). Co-existence between the traditional societies and wildlife in western Serengeti, Tanzania: its relevancy in contemporary wildlife conservation efforts. Biodivers. Conserv. *17*, 1861–1881. https://doi.org/10.1007/s10531-007-9306-z.

41. Neumann, R.P. (1995). Local challenges to global agendas: conservation, economic liberalization and the pastoralists' rights movement in tanzania. Antipode *27*, 363–382. https://doi.org/10.1111/j.1467-8330.1995.tb00285.x.

42. Authorities brutally violated Maasai amid forced evictions (2023). Amnesty Int. https://www.amnesty.org/en/latest/news/2023/06/tanzanian-authorities-brutally-violated-maasai-amid-forced-evictions/.

43. Tanzania: Maasai Forcibly Displaced for Game Reserve | Human Rights Watch (2023). https://www.hrw.org/news/2023/04/27/tanzania-maasai-forcibly-displaced-game-reserve.

44. Dawson, N.M., Coolsaet, B., Bhardwaj, A., Brown, D., Lliso, B., Loos, J., Mannocci, L., Martin, A., Oliva, M., Pascual, U., et al. (2024). Reviewing the science on 50 years of conservation: Knowledge production biases and lessons for practice. Ambio. https://doi.org/10.1007/s13280-024-02049-w.

45. Merz, L., Pienaar, E.F., Fik, T., Muyengwa, S., and Child, B. (2023). Wildlife institutions highly salient to human attitudes toward wildlife. Conserv. Sci. Pract. *5*, e12879. https://doi.org/10.1111/csp2.12879.

46. Mbise, F. (2021). Attacks on humans and retaliatory killing of wild carnivores in the eastern Serengeti Ecosystem, Tanzania. J. Ecol. Nat. Environ. *13*, 110–116. https://doi.org/10.5897/JENE2021.0908.

47. Lyamuya, R.D., Masenga, E.H., Fyumagwa, R.D., and Røskaft, E. (2014). Human–carnivore conflict over livestock in the eastern part of the Serengeti ecosystem, with a particular focus on the African wild dog *Lycaon pictus*. Oryx *48*, 378–384. https://doi.org/10.1017/S0030605312001706.

48. Broekhuis, F. (2018). Natural and anthropogenic drivers of cub recruitment in a large carnivore. Ecol. Evol. *8*, 6748–6755. https://doi.org/10.1002/ece3.4180.

49. Lindsey, P.A., Miller, J.R.B., Petracca, L.S., Coad, L., Dickman, A.J., Fitzgerald, K.H., Flyman, M.V., Funston, P.J., Henschel, P., Kasiki, S., et al. (2018). More than $1 billion needed annually to secure Africa’s protected areas with lions. Proc. Natl. Acad. Sci. *115*. https://doi.org/10.1073/pnas.1805048115.

50. Kashwan, P., V. Duffy, R., Massé, F., Asiyanbi, A.P., and Marijnen, E. (2021). From Racialized Neocolonial Global Conservation to an Inclusive and Regenerative Conservation. Environ. Sci. Policy Sustain. Dev. *63*, 4–19. https://doi.org/10.1080/00139157.2021.1924574.

51. Dowie, M. (2009). Conservation refugees: The hundred-year conflict between global conservation and native peoples (MIT Press).

52. Macdonald, E.A., Burnham, D., Hinks, A.E., Dickman, A.J., Malhi, Y., and Macdonald, D.W. (2015). Conservation inequality and the charismatic cat: Felis felicis. Glob. Ecol. Conserv. *3*, 851–866. https://doi.org/10.1016/j.gecco.2015.04.006.

53. Lev-Ari, S., and Keysar, B. (2010). Why don’t we believe non-native speakers? The influence of accent on credibility. J. Exp. Soc. Psychol. *46*, 1093–1096. https://doi.org/10.1016/j.jesp.2010.05.025.

54. Geiger, M.K., Langlinais, L.A., and Geiger, M. (2023). Accent Speaks Louder than Ability: Elucidating the Effect of Nonnative Accent on Trust. Group Organ. Manag. *48*, 953–965. https://doi.org/10.1177/10596011221117723.

55. Perrachione, T.K., Chiao, J.Y., and Wong, P.C.M. (2010). Asymmetric cultural effects on perceptual expertise underlie an own-race bias for voices. Cognition *114*, 42–55. https://doi.org/10.1016/j.cognition.2009.08.012.

56. Mathiesen, K.E., Barmoen, M., Bærum, K.M., and Johansson, M. (2022). Trust in researchers and researchers’ statements in large carnivore conservation. People Nat. *4*, 260–273. https://doi.org/10.1002/pan3.10282.

57. Sauer, K.A., Capps, D.K., Jackson, D.F., and Capps, K.A. (2021). Six minutes to promote change: People, not facts, alter students’ perceptions on climate change. Ecol. Evol. *11*, 5790–5802. https://doi.org/10.1002/ece3.7553.

58. Kidd, L.R., Garrard, G.E., Bekessy, S.A., Mills, M., Camilleri, A.R., Fidler, F., Fielding, K.S., Gordon, A., Gregg, E.A., Kusmanoff, A.M., et al. (2019). Messaging matters: A systematic review of the conservation messaging literature. Biol. Conserv. *236*, 92–99. https://doi.org/10.1016/j.biocon.2019.05.020.

59. Kusmanoff, A.M., Fidler, F., Gordon, A., Garrard, G.E., and Bekessy, S.A. (2020). Five lessons to guide more effective biodiversity conservation message framing. Conserv. Biol. *34*, 1131–1141. https://doi.org/10.1111/cobi.13482.

60. Kolandai-Matchett, K., and Armoudian, M. (2020). Message framing strategies for effective marine conservation communication. Aquat. Conserv. Mar. Freshw. Ecosyst. *30*, 2441–2463. https://doi.org/10.1002/aqc.3349.

61. Niemiec, R.M., Sekar, S., Gonzalez, M., and Mertens, A. (2020). The influence of message framing on public beliefs and behaviors related to species reintroduction. Biol. Conserv. *248*, 108522. https://doi.org/10.1016/j.biocon.2020.108522.

62. Jacobson, S.K., Morales, N.A., Chen, B., Soodeen, R., Moulton, M.P., and Jain, E. (2019). Love or Loss: Effective message framing to promote environmental conservation. Appl. Environ. Educ. Commun. *18*, 252–265. https://doi.org/10.1080/1533015X.2018.1456380.

63. Olmedo, A., Veríssimo, D., Challender, D.W.S., Dao, H.T.T., Rubino, E.C., and Milner-Gulland, E.J. (2024). Designing celebrity-endorsed behavioral interventions in conservation. Conserv. Biol. *38*, e14273. https://doi.org/10.1111/cobi.14273.

64. Boling, K.S., and Walker, D. (2021). How Race and Gender Impact the Perceived Objectivity of Broadcast Women of Color on Twitter. Soc. Media Soc. *7*, 205630512110629. https://doi.org/10.1177/20563051211062921.

65. Groggel, A., Nilizadeh, S., Ahn, Y.Y., Kapadia, A., and Rojas, F. (2019). Race and the beauty premium: Mechanical Turk workers' evaluations of Twitter accounts. Inf. Commun. Soc. *22*, 709–716. https://doi.org/10.1080/1369118X.2018.1543443.

66. Lord, K.R., Putrevu, S., and Collins, A.F. (2019). Ethnic influences on attractiveness and trustworthiness perceptions of celebrity endorsers. Int. J. Advert. *38*, 489–505. https://doi.org/10.1080/02650487.2018.1548196.

67. Kothari, A. (2021). Half-Earth or Whole-Earth? Green or transformative recovery? Where are the voices from the Global South? Oryx *55*, 161–162. https://doi.org/10.1017/S0030605321000120.

68. Trisos, C.H., Auerbach, J., and Katti, M. (2021). Decoloniality and anti-oppressive practices for a more ethical ecology. Nat. Ecol. Evol. *5*, 1205–1212. https://doi.org/10.1038/s41559-021-01460-w.

69. Tan, K. (2021). Just conservation: The question of justice in global wildlife conservation. Philos. Compass *16*, e12720. https://doi.org/10.1111/phc3.12720.

70. Pritchard, R., Sauls, L.A., Oldekop, J.A., Kiwango, W.A., and Brockington, D. (2022). Data justice and biodiversity conservation. Conserv. Biol. *36*, e13919. https://doi.org/10.1111/cobi.13919.

71. Saif, O., Keane, A., and Staddon, S. (2022). Making a case for the consideration of trust, justice, and power in conservation relationships. Conserv. Biol. *36*, e13903. https://doi.org/10.1111/cobi.13903.

72. Armstrong, C. (2023). Global justice and the opportunity costs of conservation. Conserv. Biol. *37*, e14018. https://doi.org/10.1111/cobi.14018.

73. Harris, N.C., Wilkinson, C.E., Fleury, G., and Nhleko, Z.N. (2023). Responsibility, equity, justice, and inclusion in dynamic human–wildlife interactions. Front. Ecol. Environ. *21*, 380–387. https://doi.org/10.1002/fee.2603.

74. Primack, R.B., Miller, T.K., Terry, C., Marín-Spiotta, E., Templer, P.H., Berhe, A.A., Diaz Vallejo, E.J., Hastings, M.G., Magley, V.J., Mattheis, A., et al. (2023). Historically excluded groups in ecology are undervalued and poorly treated. Front. Ecol. Environ. *21*, 363–369. https://doi.org/10.1002/fee.2613.

75. Tulloch, A.I.T. (2020). Improving sex and gender identity equity and inclusion at conservation and ecology conferences. Nat. Ecol. Evol. *4*, 1311–1320. https://doi.org/10.1038/s41559-020-1255-x.

76. Coon, J.J., Alexander, N.B., Smith, E.M., Spellman, M., Klimasmith, I.M., Allen-Custodio, L.T., Clarkberg, T.E., Lynch, L., Knutson, D., Fountain, K., et al. (2023). Best practices for LGBTQ + inclusion during ecological fieldwork: Considering safety, cis/heteronormativity and structural barriers. J. Appl. Ecol. *60*, 393–399. https://doi.org/10.1111/1365-2664.14339.

77. Bromser-Kloeden, T. (2024). Navigating environmental academia in a disabled body: an embodied autoethnography of ableism and advocacy. Disabil. Soc., 1–6. https://doi.org/10.1080/09687599.2024.2345346.

78. Amano, T., Ramírez-Castañeda, V., Berdejo-Espinola, V., Borokini, I., Chowdhury, S., Golivets, M., González-Trujillo, J.D., Montaño-Centellas, F., Paudel, K., White, R.L., et al. (2023). The manifold costs of being a non-native English speaker in science. PLOS Biol. *21*, e3002184. https://doi.org/10.1371/journal.pbio.3002184.

79. Amano, T., Berdejo-Espinola, V., Christie, A.P., Willott, K., Akasaka, M., Báldi, A., Berthinussen, A., Bertolino, S., Bladon, A.J., Chen, M., et al. (2021). Tapping into non-English-language science for the conservation of global biodiversity. PLOS Biol. *19*, e3001296. https://doi.org/10.1371/journal.pbio.3001296.

80. Maas, B., Pakeman, R.J., Godet, L., Smith, L., Devictor, V., and Primack, R. (2021). Women and Global South strikingly underrepresented among top-publishing ecologists. Conserv. Lett. *14*. https://doi.org/10.1111/conl.12797.

81. Nakamura, G., Soares, B.E., Pillar, V.D., Diniz-Filho, J.A.F., and Duarte, L. (2023). Three pathways to better recognize the expertise of Global South researchers. Npj Biodivers. *2*, 17. https://doi.org/10.1038/s44185-023-00021-7.

82. Dangles, O., Struelens, Q., Ba, M.-P., Bonzi-Coulibaly, Y., Charvis, P., Emmanuel, E., González Almario, C., Hanich, L., Koita, O., León-Velarde, F., et al. (2022). Insufficient yet improving involvement of the global south in top sustainability science publications. PLOS ONE *17*, e0273083. https://doi.org/10.1371/journal.pone.0273083.

83. Ocampo-Ariza, C., Toledo-Hernández, M., Librán-Embid, F., Armenteras, D., Vansynghel, J., Raveloaritiana, E., Arimond, I., Angulo-Rubiano, A., Tscharntke, T., Ramírez-Castañeda, V., et al. (2023). Global South leadership towards inclusive tropical ecology and conservation. Perspect. Ecol. Conserv. *21*, 17–24. https://doi.org/10.1016/j.pecon.2023.01.002.

84. Ramírez-Castañeda, V., Westeen, E.P., Frederick, J., Amini, S., Wait, D.R., Achmadi, A.S., Andayani, N., Arida, E., Arifin, U., Bernal, M.A., et al. (2022). A set of principles and practical suggestions for equitable fieldwork in biology. Proc. Natl. Acad. Sci. *119*, e2122667119. https://doi.org/10.1073/pnas.2122667119.

85. Demery, A.J.C., and Pipkin, M.A. (2021). Safe fieldwork strategies for at-risk individuals, their supervisors and institutions. Nat. Ecol. Evol. *5*, 5–9. https://doi.org/10.1038/s41559-020-01328-5.

86. Rudzki, E.N., Kuebbing, S.E., Clark, D.R., Gharaibeh, B., Janecka, M.J., Kramp, R., Kohl, K.D., Mastalski, T., Ohmer, M.E.B., Turcotte, M.M., et al. (2022). A guide for developing a field research safety manual that explicitly considers risks for marginalized identities in the sciences. Methods Ecol. Evol. *13*, 2318–2330. https://doi.org/10.1111/2041-210X.13970.

87. Griffiths, M., Mueni, F., Baker, K., and Patel, S. (2023). Decolonising spaces of knowledge production: Mpala research centre in Laikipia County, Kenya. Environ. Plan. E Nat. Space *6*, 2340–2357. https://doi.org/10.1177/25148486231156728.

88. Garnett, S.T., Burgess, N.D., Fa, J.E., Fernández-Llamazares, Á., Molnár, Z., Robinson, C.J., Watson, J.E.M., Zander, K.K., Austin, B., Brondizio, E.S., et al. (2018). A spatial overview of the global importance of Indigenous lands for conservation. Nat. Sustain. *1*, 369–374. https://doi.org/10.1038/s41893-018-0100-6.

89. Beattie, M., Fa, J.E., Leiper, I., Fernández-Llamazares, Á., Zander, K.K., and Garnett, S.T. (2023). Even after armed conflict, the environmental quality of Indigenous Peoples' lands in biodiversity hotspots surpasses that of non-Indigenous lands. Biol. Conserv. *286*, 110288. https://doi.org/10.1016/j.biocon.2023.110288.

90. O'Bryan, C.J., Garnett, S.T., Fa, J.E., Leiper, I., Rehbein, J.A., Fernández-Llamazares, Á., Jackson, M.V., Jonas, H.D., Brondizio, E.S., Burgess, N.D., et al.

(2021). The importance of Indigenous Peoples' lands for the conservation of terrestrial mammals. Conserv. Biol. *35*, 1002–1008. https://doi.org/10.1111/cobi.13620.