HOW PRIDES OF LION RESEARCHERS ARE EVOLVING TO BE INTERDISCIPLINARY

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Editorial: How Prides of Lion Researchers Are Evolving to Be Interdisciplinary

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Editorial on the Research Topic

How Prides of Lion Researchers Are Evolving to Be Interdisciplinary

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INTRODUCTION

Lions (*Panthera leo*) are one of the most charismatic, enigmatic, and polarizing species on the planet (Macdonald et al., 2015; Albert et al., 2018; Courchamp et al., 2018). Human connections to lions, as functional members of ecological communities and as icons of strength and courage, are truly cross-cultural (Schaller, 1972). Lion symbology, for instance, appears around the world, even in geographic locations outside of the species range (McCall, 1973). The images of lions adorn currency, jewelry, art, clothing, corporate logos and masonry, among others, where they are used and traded on a daily basis (Evans, 1896; Olupona, 1993; Mwangi, 2002). People experience strong emotions when in the company of lions whether that be at zoos, from the relative safety of a safari vehicle, or while grazing livestock on open rangelands in Africa or India (Hemson et al., 2009; Goldman et al., 2010; Meena et al., 2014). Lions clearly command reverence and yet, as humans, we have grown acutely accustomed to conflict with this species. Fears relating to insecurity and loss of livestock motivate swift and aggressive retaliatory responses to lions (Patterson et al., 2004; Dickman, 2010; Millspaugh et al., 2015). Thus, lions seem capable of captivating and scaring humans in equal measure. Perhaps not surprisingly then, here in the twenty-first century, lions are a species of immense conservation concern and one that has defied numerous efforts toward population restoration outside of inviolate protected areas. Lions have experienced precipitous and unabated population declines over the last 100 years causing the conservation community to periodically downgrade the species conservation status (Bauer et al., 2015; Riggio et al., 2015).

The conservation of lions therefore presents a thorny challenge. In their contributing paper to this special issue, Montgomery et al. identify that human-lion conflict is a highly complex issue involving not only the two implied domains (i.e., humans and lions), but also characteristics of livestock and human culture, factors associated with wild prey populations, and abiotic conditions in the environment. This paper articulates that the issue of human-lion conflict is one that is clearly multifaceted and multidimensional. Several calls among the scientific community have demonstrated the utility of evaluating complex problems with research teams that are multidisciplinary, interdisciplinary, and, hopefully at some point, transdisciplinary (White and Ward, 2010; Rylance, 2015). Thus, the objective of this special issue is to highlight the ways in which research teams assessing human-lion conflict and those assessing lion ecology, more broadly, have been, and are evolving to be, interdisciplinary. This special issue features 11 papers exploring these topics across the range of lions from West Africa to East Africa and from South Africa to the Greater Gir Landscape of India.

In this editorial piece, we frame three of the major questions pursued among these papers. The first question examines the degree to which lion research has been interdisciplinary. Several papers in this special issue quantified various indicators of interdisciplinarity among teams of lion researchers historically. The second question assesses the role of interdisciplinarity in lion conservation. These papers examine spatial variation in conservation decision-making involving topics such as trophy hunting, human-lion conflict mitigation, and cultural tolerance of lions. The final question evaluates how lion research can become more interdisciplinary. Technological advancements are presented as a means to improve our understanding of lion ecology and develop solutions for human-lion conflict. We ground the discussion of these three major questions within the context of renewed efforts to implement innovative conservation strategies to improve the population trajectories of lions throughout their range.

HAS LION RESEARCH HISTORICALLY BEEN INTERSDISCIPLINARY?

Exploring the extent to which lion research has been interdisciplinary historically, several papers in this special issue evaluated various aspects of team science. Scientific assessments of team science represent a comparatively recent area of inquiry examining the impacts of team composition and demographics on the outcomes and impact of collaborative research (Stokols et al., 2008; Ledford, 2015). To quantify the levels of interdisciplinarity inherent to historic research on human-lion conflict, Montgomery et al. used team science tools to review peer-reviewed research on this topic. They found that human-lion conflict research increased exponentially from 1990 to 2015. Despite this growth however, the number of co-authors on the resultant publications was highly consistent over time. There were just 3.28 (SD = 0.19) co-authors per publication. When evaluating the disciplinary identities of these co-authors, Montgomery et al. determined that almost all derived from three highly-related disciplines (i.e., biology/ecology/zoology, wildlife management/conservation, and environmental science). Co-authors from the humanities or social sciences, were particularly underrepresented among this literature as they occurred among <4% of the co-authors. These observations suggest that researchers of human-lion conflict have not mirrored the complexity inherent to the subject matter. Importantly however, these low levels of interdisciplinary do not speak solely to a failure of lion biologists to engage with humanities or social science colleagues. Rather, they speak to broader problems associated with interdisciplinary team science writ large (Bromham et al., 2016). Namely, low ability to attain sustainable funding, variation among currencies of evaluation, and inconsistencies in expectations for research output are widely detrimental to interdisciplinary science (Lélé and Norgaard, 2005; Eigenbrode et al., 2007).

The species range of lions is divided across some 18 countries and two continents (Bauer et al., 2016). The amount of research and the allocation of conservation effort varies considerably across that extent. Sobratee and Slotow conducted a review of South African-led lion research between the years 1990 and 2018. They found that interdisciplinarity among this research grew 3- and 6-fold growth with each advancing decade. Interdisciplinarity was particularly manifest when evaluating the application of research methodologies and technologies. Sobratee and Slotow did note considerable power dynamics inherent to the research that they evaluated. These power dynamics were illustrated by low levels of first authors that were female or derived from portions of Africa outside of South Africa. The authors discuss the underlying power differentials associated with these observations. Trends such as these however, are not exclusive to South African led research on lions.

Bauer et al., for instance, detected similar patterns when evaluating lion research across Africa. The authors reviewed 615 lion papers and looked in detail at co-author demographics. They detected 199 authors that contributed to ≥ 3 papers. Approximately 70% ($n = 138$ of 199) of these co-authors were male. However, despite the fact that this research occurred in Africa, only 30% ($n = 61$ or 199) of these co-authors were African nationals and just a fraction of those authors were non-white. Bauer et al. discuss the evident barriers to diversity that exist among lion research. A problematic consequence of these patterns that Bauer et al. discuss is the dearth of lion expertise within African countries. They issue an urgent call to action to change the demographics of lion research under what they term a “shared responsibility.”

While Montgomery et al. demonstrated the five dimensions inherent to human-lion conflict, and human-carnivore conflict more broadly, Beck et al. demonstrate the inherent interconnectedness of the variables that define these five dimensions. They present a conceptual model with a number of overlapping and interacting factors that move between and across these dimensions of conflict. Beck et al. discuss how this conceptual model can be used to prioritize the preparation of research teams poised to respond to challenges inherent to human-lion conflict. They provide an example of how to put this process into action so as to illustrate the application of this conceptual model. Beck et al. also provide a series of recommendations about how barriers to interdisciplinarity can be overcome in human-lion conflict research with benefits to lion conservation and the improvement of human well-being. While this suite of papers demonstrates that interdisciplinarity has been rather low historically, current research on lions reflects the critical need for interdisciplinary team science promoting improved understandings of lion ecology with subsequent benefits to lion conservation.

WHAT IS THE ROLE OF INTERDISCIPLINARITY IN LION CONSERVATION?

The next set of papers examined the role of interdisciplinarity in conservation work across the range of lions. While the vast majority of remaining lions occur in Africa, a remnant population of Asiatic lions (*Panthera leo persica*) continue to inhabit the Greater Gir landscape of India. Jhala et al. discuss the history of Asiatic lions in India. This paper compares lion ecology and sociology between India and Africa. This is an apt comparison given that it has been suggested that cultural tolerance of lions is higher in the Greater Gir than it is across the species African range (Banerjee et al., 2013; Meena et al., 2014). Jhala et al. explore this variation and discuss the important conservation actions (such as national park establishment and community-based tourism benefits) that may be necessary to secure Indian lion populations for future generations.

In a novel assessment of several dimensions that could reduce human-lion conflict, Ng'weno et al. examine the impact of livestock and wild prey interactions on lion ecology. They looked specifically at apparent competition associated with Jackson's hartebeest (*Alcelaphus buselaphus lelwel*) and plains zebra (*Equus quagga*) that are preyed upon by lions in Laikipia County, Kenya. The analysis found that lions selectively killed hartebeest while they took zebra at rates to be expected given their relative abundance. Ng'weno et al. detected zebra use of abandoned livestock corrals, which were comparatively higher in nutrients, and a positive correlation between hartebeest survival and distance from these corrals. The authors discuss the ways in which livestock corrals could be logically distributed to conserve hartebeest, a species of conservation concern, within this coupled natural and human system. Ng'weno et al. articulate a series of conservation implications from this research including the impact of managed livestock grazing on wild prey populations.

In an applied analysis, Kushnir and Packer explore patterns of risk perception among Tanzanian communities vulnerable to lion attack. This is a region of the world that experiences intense human-lion conflict. The authors quantified ∼1,000 lion attacks on people in Tanzania between 1990 and 2007. Via the implementation of questionnaire surveys, Kushnir and Packer found that perceptions of risk from lions among local people were far higher than the actual risk of attack. Furthermore, many of the respondents viewed risk from lions to be comparable to those deriving from disease (i.e., malaria and AIDS) or environmental conditions (i.e., drought and famine). Kushnir and Packer place these observations within the context of lions being able to exert considerable fear in people. For example, while the probability of lion attack is very low, the rate at which people die following an attack (66%) is high.

Another important assessment of the social dimensions inherent to lion research involved the point source response of large swaths of global society to the trophy killing of Cecil the lion in Zimbabwe in 2015 (Macdonald et al., 2016). As an example of interdisciplinarity, Buhrmester et al. convened a team of researchers from anthropology, political science, and conservation biology to assess the demographics and actions of private donors that supported the Wildlife Conservation Research Unit (WildCRU) at Oxford University, responsible for studying Cecil in Hwange National Park, in the wake of Cecil's killing. Buhrmester et al. implemented a longitudinal survey to examine the social psychology associated with motivations to give monetary support to lion conservation. They found signatures of social cohesion in the private donor behavior that were representative of identity fusion. Despite the fact that Cecil was a lion living in Zimbabwe before being killed by a trophy hunter, Buhrmester et al. found that private donors from around the world were able to relate to the animal across spatio-temporal dimensions and that the sense of relatability that was formed, translated to a powerful call to action. These observations, and others like it among this suite of papers, were only made possible by the formation of interdisciplinary research teams bringing together scholars from the biological sciences, social sciences, and humanities in the pursuit of coordinated inquiries around lion conservation.

HOW CAN LION RESEARCH BECOME MORE INTERDISCPLINARY?

The study of lion ecology, much like the study of large mammals more broadly, has been defined by advancements in technology. Such advancements for wildlife research are inherently dependent upon interdisciplinary research involving wildlife ecologists, engineers, physicists, technicians, and many others. The growth of technology in lion research, particularly within the context of the Serengeti Lion Project, is the subject of Craig Packer's sole-authored paper in this special issue. In that paper, Packer provides a chronology of the expansion of research focus from the time that the project was initiated by George Schaller in 1966 to the end of Packer's 40-year involvement in the study. The paper demonstrated how teams of interdisciplinary colleagues were prepared to study the evolution of lion social behavior, assess lion mating strategies, develop applied solutions for canine distemper virus (which spread from domestic dogs to the Serengeti and Ngorongoro Crater lion populations), and manage the big data deriving from a broad scale camera trapping system termed Snapshot Serengeti. Packer ends the paper by discussing the role of interdisciplinarity in developing progressive solutions capable of conserving lions in a dynamic twenty-first century.

Wijers et al. provide a case study of the technological growth of lion research. An emerging area of inquiry in the field of ecology examines the soundscape, or acoustic landscapes (Pijanowski et al., 2011). In their paper, Wijers et al. demonstrate how bio-loggers could be developed to record audio of lions. When combined with GPS and accelerometer information, these lion-borne acoustic sensors not only revealed interesting information on the acoustic range of lions but also provided an accurate means to create a behavioral ethogram. Behaviors revealed via these bio-loggers included drinking, eating, and three different movement states (stationary, slow moving, and fast moving). Wijers et al. discuss the far-ranging applicability of this technology across the field of animal behavior.

In Botswana's Okavango Delta, Weise et al. present a technological system that alerts local communities to the advancing presence of tagged lions. This version of a "geofence" was piloted across a 24-month period where alerts, in the form of text messages to livestock-owners' phones, were issued in response to the movement of nine study lions. Weise et al.

describe the human actions that corresponded to the information of lion presence detected on this system. These included herder modification of livestock space use on the rangelands, increasing vigilance in herding practice, protecting livestock in kraals overnight, and tending fires to act as a deterrent to lions. Weise et al. simultaneously evaluated the efficacy of these actions as well as the satisfaction of livestock-owners. They found that the changes in human behavior associated with the information deriving from this system significantly decreased lion depredation of livestock. Furthermore, livestock-owners were far more satisfied with this alert system than they were with *post-hoc* financial compensation schemes. Weise et al. provide a balanced discussion of the opportunities and challenges that are inherent to the application of this technology and expound upon the implications of this research for lion conservation. These three papers clearly demonstrate the fundamental role of interdisciplinarity in developing novel and original technologies to facilitate the research-informed conservation of lions.

CONCLUSION

Lions are a species of immense conservation concern across the globe. Despite that concern however, it remains firmly in doubt whether lions will continue to be functional components of the ecosystems that they inhabit 25–50 years from now. Conflict with humans is a powerful driver of lion population declines. Once weakened by conflict, lions become even more vulnerable to swift declines via the concurrent mechanisms of habitat loss, population isolation, prey depletion, and disease. Human-lion conflict is a highly complex issue involving five dimensions (Montgomery et al.), with scores of interacting components within each dimension (Beck et al.). What is clear is that the livelihood of lion populations is dependent upon teams of interdisciplinary scientists, stakeholders, policy-makers, and local communities productively collaborating to confront the challenges inherent to conserving this species. Though the markers of interdisciplinary team science within this context have been rather low historically, present and future trends demonstrate a shift in the structure of lion research. Self-reflective questions are being assessed (Montgomery et al., Beck et al.), weaknesses highlighted and solutions derived (Bauer et al., Sobratee and Slotow), technological advancements are being embraced (Packer, Wijers et al., Weise et al.), and new and productive partnerships are being forged (Jhala et al., Ng'weno et al.). Thus, the papers in this special issue provide clear indications that research on human-lion conflict is rapidly evolving and that this evolution will be part of securing lion populations for future generations.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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REVIEW
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Examining Evident Interdisciplinarity Among Prides of Lion Researchers

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Lions (*Panthera leo*) have experienced dramatic population declines in recent decades and today, inhabit just a fraction of their historic range. The reasons behind these declines are many, but conflict with humans, principally motivated by lion depredation of livestock, is among the most influential. Recent calls within the scientific community have identified that wicked problems like these should be addressed using interdisciplinary approaches. Here we examined the extent to which human-lion conflict research has been interdisciplinary. We conducted an extensive review of the literature and uncovered 88 papers, published between 1990 and 2015, that assessed human-lion interaction and the ecology of lions exposed to anthropogenic disturbance. While human-lion conflict research experienced near-exponential growth (y = 8E-194e0.222x, $R^2 = 0.76$) across this time period, the number of co-authors engaged in this research changed very little ($\bar{x} = 3.28$, se = 0.19). Moreover, co-authors of this research tended to be affiliated with units from just three highly-related STEM disciplines (biology, wildlife management, and environmental science). Comparatively, co-authors affiliated with units in the humanities and social sciences occurred in <4% of all papers examined. Our analysis also presents a novel framework that positions human-lion conflict research as having not two dimensions, as has been commonly conceptualized, but five dimensions. These dimensions include not only the human and the lion dimensions, but also the livestock, wild prey, and environmental dimensions. None of the papers that we evaluated concurrently studied all five of these dimensions to determine their impact on human-lion conflict. Furthermore, despite the fact that human-lion conflict research was primarily developed by co-authors from STEM disciplines, the most common dimension evaluated was the human dimension which requires social science and humanities expertise. Our analysis indicates that interdisciplinarity among human-lion conflict research has historically been low. These low levels of interdisciplinarity observed from 1990 to 2015 however, are not necessarily representative of the ongoing efforts to develop more inclusive research teams. Thus, we discuss the implications of this research for the development of sustainable solutions to conserve lions and preserve human well-being and identify potential avenues forward to create more interdisciplinary prides of lion researchers.

Keywords: conservation, human-lion conflict, interdisciplinary, lion, Panthera leo

INTRODUCTION

Lions (*Panthera leo*) are a highly enigmatic and charismatic species capable of capturing the attention of the scientific community and broader public alike. There is perhaps no better example of that capability than the societal response to the killing of Cecil the lion by a hunter in Zimbabwe in July of 2015. Less than a month later, stories in the editorial media describing this incident reached a peak of 12,000/day while hits on social media peaked at >87,000/day (Macdonald et al., 2016). Thus, in the twenty-first century, in large part due to their iconic and integral role (i.e., fundamental to the trophic systems in which they reside), lions are a species of unusually special conservation concern (McNeely, 2000; Dickman et al., 2011; Lindsey et al., 2012; Ripple et al., 2014; Macdonald et al., 2015). Once common across all of Africa, as well as portions of Europe and Asia, lions are restricted to fragmented populations in sub-Saharan Africa and one very isolated population in west India (Riggio et al., 2013; Henschel et al., 2014; Meena et al., 2014; Bauer et al., 2015). Lions now occur in just 8% of their historic range and have experienced an estimated 43% population reduction in the past 20 years (Bauer et al., 2015). Predictions suggest there are now ∼25,000 lions in Africa with only ∼500 individual lions remaining in India (Singh and Gibson, 2011; Bauer et al., 2015). Further, within the next 20 years, lions could decline by an additional 50% in Western-Central and East Africa, positioning the species itself on the cusp of extinction (Henschel et al., 2014; Bauer et al., 2015).

The reasons behind these declines are many including habitat loss, climate change, hunting, disease, and human conflict (Loveridge et al., 2016; Macdonald, 2016). Although all of these elements have contributed to the 1996 downgrading in conservation status of lions (i.e., from *near threatened* to *vulnerable* by the International Union for the Conservation of Nature—IUCN; Bauer et al., 2015), there is one element, in particular, that will determine whether lions continue to inhabit wild places in future. That element is human-lion conflict. Conflict, whereas the term is reductive and unsatisfactorily narrow in its depiction of just a portion of human-wildlife interaction (Conover, 2002; Madden, 2004; Nyhus, 2016), is illustrative of an important part of that interaction. Threats to human security and competition for resources can promote human-carnivore conflict (Millspaugh et al., 2015) with implications for carnivore conservation and human well-being. This is an age-old problem with clear evidence that human evolution itself, has been shaped by conflict with carnivore species such as lions (Bunn and Ezzo, 1993; Treves and Naughton-Treves, 1999; Camarós et al., 2016).

Conflict between humans and carnivores often involves competition over prey species, whether they be wild-living or domesticated (Patterson et al., 2004; Graham et al., 2005; Dickman, 2010). In the present day, this conflict tends to derive from real or perceived depredation of livestock. Lions, for instance, prey upon a variety of domestic livestock including cattle, goats, sheep, and donkeys and can attack during both daytime (when livestock are often on the grazing lands) and nighttime (when livestock are typically herded together in livestock enclosures, i.e., bomas, kraals, corral, or stockade) periods (Ogada et al., 2003; Kissui, 2008). The current range of lions primarily overlaps with developing nations where livestock-keepers are particularly dependent upon, and vulnerable to, the loss of- livestock (Thornton et al., 2002; Bank, 2009; Thornton, 2010). Thereby, livestock depredation can be fearsome, dispiriting, and economically crippling (Treves and Karanth, 2003; Inskip and Zimmermann, 2009; Miller, 2015). Experiences of this type foster soundly negative perceptions of lions among affected human communities (Treves and Karanth, 2003; Woodroffe and Frank, 2005; Kissui, 2008; Dickman, 2010; Dickman et al., 2014). Rapid increases in meat production (a tripling between 1980 and 2002 in developing nations) likely intensifies the potential for lion-livestock interaction (Thornton, 2010; Bauer et al., 2015). Thus, developing solutions for human-lion conflict is of paramount importance for the conservation of lion populations and the improvement of human well-being.

At the coarsest resolution, human-lion conflict can only occur where lions and people interact. However, spatio-temporal patterns of human-lion conflict are considerably more complex than that. Evident variation in hotspots of human-lion conflict illustrate that the factors that promote conflict are highly complex (Baker et al., 2008; Kissui, 2008; Dickman et al., 2014; Miller, 2015). This complexity problematizes efforts to prescribe robust interventionist practices meant to alleviate that conflict. Close examination of human-carnivore conflict broadly, and human-lion conflict more specifically, reveals there are five, not two (as the phrase implies), dimensions that play a role. Spatio-temporal patterns of conflict depend not only on humans and carnivores, but also on livestock, wild prey, and environmental factors. The five dimensions of human-carnivore conflict are (**Figure 1**):

1) the carnivore (hereafter referred to as the "lion") dimension
   - including information relating to the distribution, abundance, and behavior of carnivores

FIGURE 1 | Human-carnivore conflict broadly, and human-lion conflict more specifically, is an inherently interdisciplinary issue with five dimensions that broadly determine the intensity of conflict.

2) the livestock dimension
 - including information relating to the distribution, abundance, and behavior of livestock
3) the wild prey dimension
 - including information relating to the distribution, abundance, and behavior of wild prey
4) the human dimension
 - including information on human perceptions/attitudes, practices, finances, and policies
5) the environmental dimension
 - including information relating to weather, seasonality, and land cover.

Given that five dimensions contribute to spatio-temporal patterns and intensity of human-lion conflict, this ecological phenomena is inherently multidimensional.

Recent calls among the scientific community have identified the fundamental need to address multidimensional, or *wicked*, problems via multidisciplinary and interdisciplinary research (Mascia et al., 2003; White and Ward, 2010; Ledford, 2015; Rylance, 2015). Indicative of the importance of these approaches the journal Nature devoted an entire issue to explorations of multi-, inter-, and trans-disciplinary research in 2015 (volume 525, issue 7569). Multidisciplinary research is often defined as research that incorporates scholars and methods from multiple disciplines to study a problem or system, but the different disciplinary perspectives remain largely distinct; moreover, one discipline typically dominates the others (Eigenbrode et al., 2007; Miller et al., 2008). Interdisciplinary research is often defined as incorporating deeper integration between different perspectives, such that investigators develop greater appreciation for each other's methodological approaches and sometimes develop new questions and methods (Eigenbrode et al., 2007; Miller et al., 2008). Transdisciplinary research involves the deepest integration of disciplinary perspectives, such that the individual disciplines are ultimately transcended and researchers develop new, unifying epistemological perspectives (Eigenbrode et al., 2007; Miller et al., 2008).

It remains to be seen whether completely new epistemological frameworks and categories will arise (thereby generating transdisciplinary research), but it seems unlikely that the complexity of the problems generated by human-lion conflict can be solved without interdisciplinary research that extensively incorporates and integrates insights from multiple disciplinary perspectives to confront the ecological and social components of the problem (Macdonald et al., 2010; White and Ward, 2010; Suryawanshi et al., 2013; Soh et al., 2014; Redpath et al., 2015; Angelici, 2016; Pooley, 2016; Macdonald and Chapron, 2017). Within this context, our study objectives were to:

i) Examine the extent to which research on human-lion conflict has been interdisciplinary by deploying an extensive review of the literature on this topic published between 1990 and 2015.
ii) Discuss the potential consequences of the observed levels of interdisciplinary on lion conservation and human livelihood improvement.

iii) Use the information garnered from this review to codify the manner in which human-lion conflict research could be shaped to be more interdisciplinary in future.

Evaluations of this type are important because they can quantify existing approaches to research and present the ways in which solutions are framed. Lions are among the most conspicuously social species within the family *Felidae* (Macdonald et al., 2010). That extreme in behavior, and doubtless their remarkable charisma (Macdonald et al., 2015), has attracted extensive study. Thus, our intent was to examine whether the willingness to be interdisciplinary among prides of lion researchers mirrors the gregariousness of their study species.

MATERIALS AND METHODS

Literature Review

We conducted an extensive search of the related literature in January of 2016. We carried out this search among four databases including Web of Science (WoS) Core Collection, Scopus, Wildlife and Ecology Studies Worldwide (WESW), and the search engine Google Scholar. We engineered our search across multiple databases to ensure that the results were representative of the literature output as a whole. Each database was searched a total of three times (primary, secondary, and tertiary searches), with each subsequent search introducing additional search terms to further narrow the results. The search structure and terms remained consistent across searches in the three commercial databases, but the searching limitations inherent in Google Scholar required additional restrictions to the exact search parameters used.

Searches within the WoS, Scopus, and WESW databases were limited to title, keyword, and abstract. Identical search terms were used in the same sequence across the three databases. The primary search terms used were "human lion livestock" AND "panthera leo." The second search added the term "conflict" to the initial terms and the tertiary search added "depredation" to the already used terms. The primary terms used for the Google Scholar search were "human lion conflict" as a phrase search to limit the results to those featuring that exact phrase. The secondary and tertiary searches built on the baseline by adding "panthera leo" and then "depredation" respectively. Due to the broad range of results provided from the Google Scholar searches and the lack of limiting functionality, we curated the results to remove non-peer-reviewed and abstract-only objects, duplicates, and annotated bibliographies.

Evaluating the Dimensions of Human-Lion Conflict Research

We then reviewed this literature to determine the applicability of each paper to human-lion conflict research. We recorded the stated research objective for each paper and excluded those papers that were not relevant to human-lion conflict research. After this exclusion process, we read each paper in detail. We documented the country where the study took place and then recorded whether the paper addressed each of the five dimensions of human-lion conflict. We documented whether the paper studied each dimension (0, 1). In cases where that dimension was studied, we recorded the exact research technique used. Multiple research techniques could be used for studying any given dimension. We then calculated a Spearman rank correlation matrix to determine the degree of relatedness among the tendency for researchers to address multiple dimensions in a given paper.

Popular Literature

We also conducted a search of the popular literature in December 2016. The search was carried out in the database LexisNexis Academic. The subject was limited to the *All News* setting and the advanced search option source type was set to include the following categories: newspapers, major world publications, magazines, wire services, blogs, business and industry news, university newspapers, U.S. newspapers, and webnews. The date range for the search was limited to 1990-2015. The search terms were modified to broaden their scope given the lack of standardized vocabulary usage in popular writing. The terms that we used were "human lion conflict Africa."

Co-author Analyses

We next conducted co-author analyses to determine the level of interdisciplinarity and multidisciplinarity among the papers addressing human-lion conflict. Co-author analyses are an ideal method for calculating interdisciplinarity and multidisciplinarity since these measures primarily address research practice rather than the content of a paper (Schummer, 2004). We excluded all theses, dissertations, and technical reports from this part of the study given a lack of co-author information. Co-authors from non-governmental organizations (NGOs), private industry, and in some cases governmental organizations, were difficult to place into a single discipline strictly using co-author affiliations. Thus, for NGOs and the private industry, we additionally used internet searches to determine a statement of purpose for each organization so as to facilitate the placement of co-authors into a given discipline. As governmental organizations often perform research on a variety of disciplines, we required a department to be stated within the co-author affiliation so as to place that co-author within a specific discipline. If this information was missing, we excluded that co-author from the disciplinary analyses. Additionally, when multiple affiliations were given for a single author we strictly recorded the primary affiliation. However, if the primary affiliation was ambiguous, we used additional affiliations to clarify geography, institution, and/or discipline.

To measure multidisciplinarity, we developed a count of the number of disciplines represented in each paper, as determined by the co-author affiliations (see Schummer, 2004). We used this information to calculate a Multidisciplinarity Index (M), observing the stated threshold of 5% (Schummer, 2004). This technique facilitates comparisons of the number of disciplines involved among the co-authorship in $\geq$5% of human-lion conflict literature. This metric is created via the following equation:

$$M^{0.05} = \text{count } [c_i] \text{ if } c_i > 0.05 \quad (1)$$

$$c_i = n_i/N$$

where c_i was the relative size of the ith discipline. The number of papers having at least one co-author in the ith discipline was denoted by n_i, and the total number of papers was represented by N. Next, the relative size of the largest discipline (c^{max}) can be calculated by:

$$c^{max} = \text{Max } [c_i] \quad (2)$$

To calculate the level of interdisciplinarity, we assessed the number of papers that were co-authored by individuals from more than one discipline. We calculated this metric for papers having co-authors that hailed from ≥ 2 disciplines (I^2) and again for papers having co-authors from ≥ 3 disciplines (I^3). Herein:

$$I^2 = \text{the number of papers co} - \text{authored by individuals from} \geq 2 \text{ disciplines}/N \quad (3)$$

$$I^3 = \text{the number of papers co} - \text{authored by individuals from} \geq 3 \text{ disciplines}/N \quad (4)$$

Next we built an interdisciplinarity matrix which displayed all possible combinations of the collaborating disciplines. Here, $n_{i,k}$ represents the number of papers that included at least one co-author from the ith and kth disciplines. We then calculated bi-disciplinarity coefficients ($c_{i,k}$) for each combination of disciplines as a function of:

$$c_{i,k} = n_{i,k}/N \quad (5)$$

It is worth noting that the diagonals of the resultant interdisciplinarity matrix represent the relative number of monodisciplinary papers for each respective discipline. Lastly, we can determine how often each discipline participates in interdisciplinary collaboration when conducting human-lion conflict research (si_i) using the following equation:

$$si_i = \sum_{k \neq i} c_{i,k}/c_i \quad (6)$$

In addition to evaluating the country in which the field research on human-lion conflict occurred, we also assessed the geographic location of each co-author's affiliation to get a sense of the degree of apparent cross-regional collaboration. While indicative of the co-author's geographic institutional affiliation at the time that the paper was published, this information does not in any way account for a co-author's country of origin.

Finally, we conducted a keyword analysis to determine the ways in which co-authors of human-lion conflict research describe their papers. We developed a database of all of the keywords used among the resultant human-lion conflict literature. Then using word cloud techniques we graphically represented the results of this analysis where the size of the keyword represented the intensity with which it was used across the literature.

RESULTS

We returned 158 unique lion research papers from our primary, secondary, and tertiary searches of literature published between 1990 and 2015 (**Figure 2A**). These papers derived from examination of four different search engines including Google Scholar, WoS, Scopus, and WESW (Figure S1). The baseline search terms ("human," "lion," and "livestock") generated the largest number of papers for each search engine with the number decreasing as subsequent search terms were added in secondary (baseline + "panthera leo") and tertiary searches (baseline + "panthera leo" and baseline + "panthera leo" + "depredation"; Figure S1). Google Scholar returned the largest number of papers, followed by WoS, Scopus, and finally WESW (**Figure 1**).

Among this set of papers, 70 were not specifically applicable to human-lion conflict research. We excluded papers when their stated research objectives were inconsistent with human-lion conflict. These papers tended to explore aspects of lion ecology irrespective of their relationship with people. We also excluded papers if they were pure reviews, primarily assessed trophy hunting of lions, examined lions in the paleological record, or mentioned lions but the focus was another species (e.g., hyenas, leopards, cheetahs). After removing these 70 papers, we retained 88 papers for examination of human-lion interaction and lion ecology in relation to sources of anthropogenic disturbance.

Research on human-lion conflict grew dramatically from 1990 to 2015 (**Figure 2A**), a trend that was consistent regardless of the search engine used (Figure S1). An exponential model of these temporal trends (y = 8E-194e0.222x) yielded a close fit to the data ($R^2 = 0.76$), suggesting growth in this research area was near-exponential from 1990 to 2015. All search engines demonstrated that research on the topic of human-lion conflict was virtually non-existent in the 1990's. Lions were downgraded by the IUCN Red List from threatened to vulnerable in 1996. Yet, it was not until the mid-2000's and into the 2010's that the research effort substantially expanded (Figure S1). For example, from 2013 to 2015, an average of 13.3 papers addressing human-lion conflict were published annually.

We found that the growth of research on human-lion conflict corresponded with growth in the popular literature coverage of conflicts between people and lions (**Figure 2B**). Furthermore, despite the research effort and corresponding media attention, the global population of lions continued to decline rapidly across this time period (**Figure 2C**). While these are admittedly coarse population estimates, between 1990 and 2015 lion populations reduced by almost half (Bauer et al., 2015; **Figure 2C**). Across

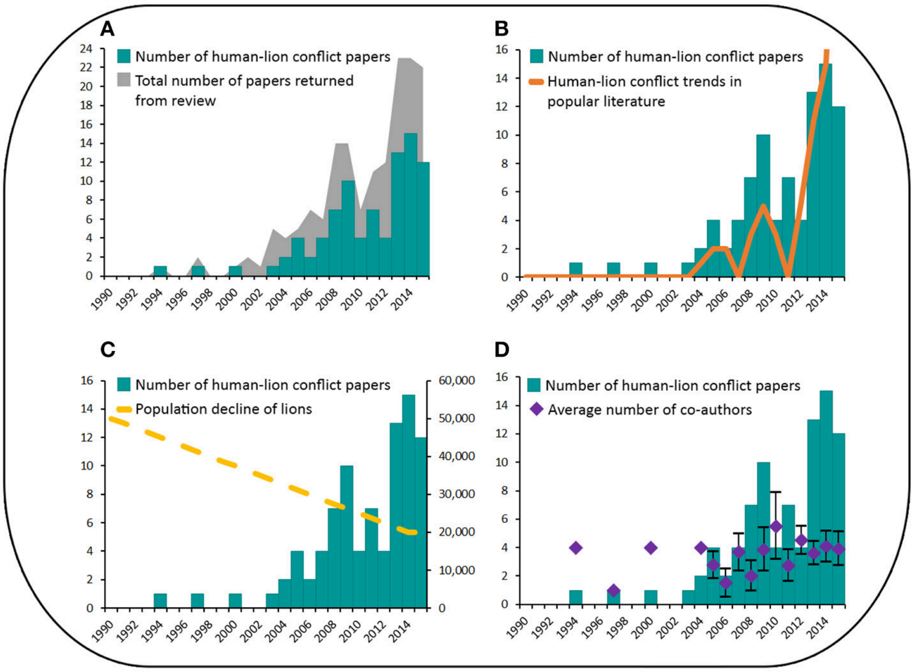

FIGURE 2 | Temporal trends in the number of human-lion conflict papers from 1990 to 2015 in relation to **(A)** the total number of papers returned from our extensive literature review, **(B)** trends in human-lion conflict in the popular literature, **(C)** the downward trajectory of lion (*Panthera leo*) populations, and **(D)** the average number of co-authors of associated with those papers.

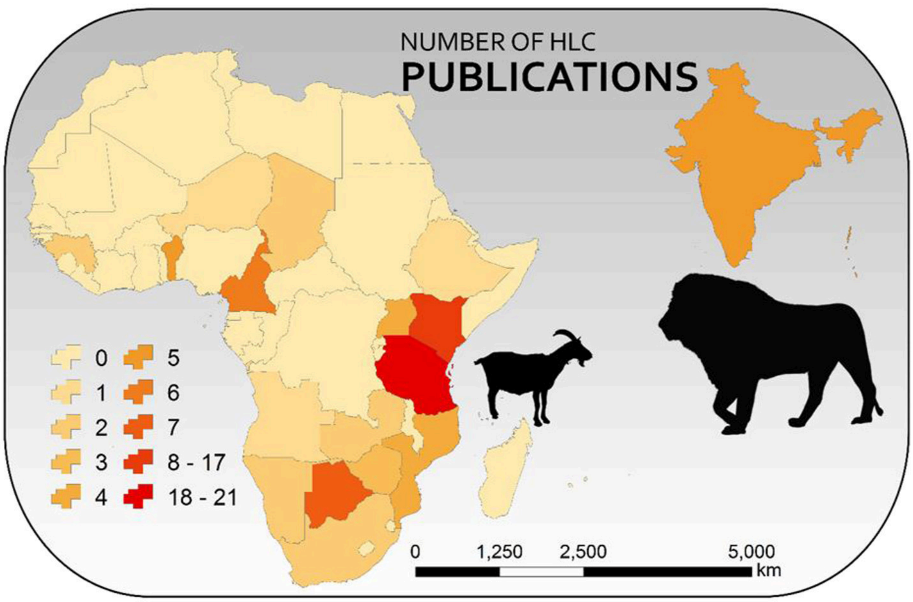

FIGURE 3 | The country location of the field component of human-lion conflict research. The figure depicts spatial variation in the number of papers evaluating human-lion conflict from 1990 to 2015.

that same period however, the number of co-authors engaged in human-lion conflict research changed very little (**Figure 2D**). While the range in the number of co-authors engaged in human-lion conflict research was between one and nine, the mean was 3.28 with a relatively narrow standard error on the estimate (se = 0.19), demonstrating consistency over time (**Figure 2D**).

The human-lion conflict field research was positioned across 16 countries in sub-Saharan Africa as well as India. The majority

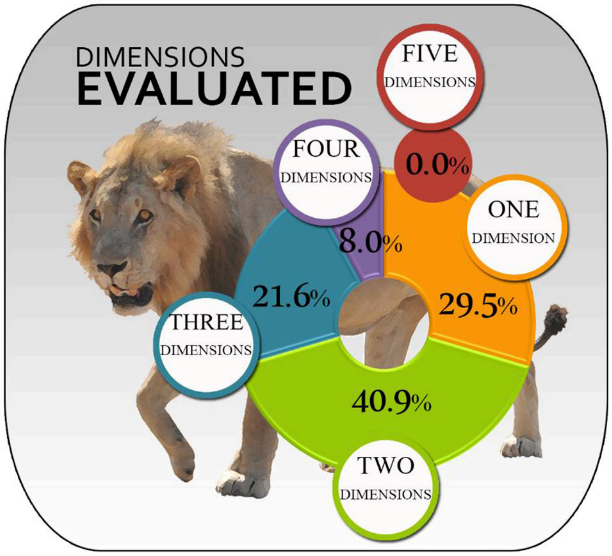

FIGURE 4 | Evidence of interdisciplinarity in human-lion conflict research. The proportion of the human-lion conflict papers published from 1990 to 2015 that concurrently evaluated multiple dimensions.

of that research occurred in East Africa (**Figure 3**). Tanzania ($n =$ 21) had the highest number of human-lion conflict papers with Kenya following in second position ($n = 17$). Thereafter the number of human-lion conflict papers declined rapidly with no one country recording greater than seven total papers from 1990 to 2015 (**Figure 3**).

The dimension that was most commonly evaluated was the human dimension ($n = 46$, 52.3% of the papers). The lion dimension was next ($n = 42$, 47.7%) followed by the environmental dimension ($n = 38$, 43.2%), and then the livestock dimension ($n = 33$, 37.5%). Finally, the dimension that was least likely to be assessed was the wild prey dimension ($n = 24$, 27.3%). The vast majority of these papers evaluated only one ($n = 26$) or two ($n = 36$) of the human-lion conflict dimensions at a time (**Figure 4**). Far fewer papers concurrently evaluated three dimensions ($n = 19$) and a small minority of papers assessed four dimensions ($n = 7$; **Figure 4**). No paper that we reviewed assessed all five dimensions of human-lion conflict concurrently (**Figure 4**). Furthermore, we detected no correlation among the dimensions that were evaluated (Table S1). The most likely tendency ($|r| = 0.59$; Table S1) was to study the human dimension and the lion dimension in the same paper.

Within each dimension, the exact research technique used also varied (**Figure 5**). There were seven primary techniques used to study the lion dimension, five for the livestock dimension, nine for the wild prey dimension, five for the human dimension, and three for the environmental dimension (**Figure 5**). The majority of papers that evaluated the lion dimension used telemetry to track movement and map the habitat/resource selection of lions (**Figure 5**). Other techniques included spoor surveys, call-up surveys, continuous follows, camera traps, examinations of lion dental records, and human surveys gauging lion ecology. The most common technique used to assess the livestock dimension was surveys (aerial, head counts, reports/interviews of number of livestock owned) of livestock herds, followed by examination of depredation locations, participatory mapping of livestock movement, telemetry, and literature surveys to reveal information about livestock ecology (**Figure 5**). There were a diversity of techniques used to assess the wild prey dimension and no single one was predominant (**Figure 5**). The human dimension and the environmental dimension were considerably more consistent. Though the human dimension was evaluated using camera traps, reported data on human populations, structured survey designs, and human space use mapping, by far the most common technique was semi-structured human surveys (**Figure 5**). Finally, to study the environmental dimension, co-authors mapped climate/weather/seasonal conditions, evaluated land cover characteristics, and calculated proximity metrics (e.g., distance to features of interest including, but not limited to, protected area boundary, water sources, and habitat edges; **Figure 5**).

Co-authors of these human-lion conflict papers derived from a set of nine total disciplinary categories (**Table 1**). Three disciplines (biology/ecology/zoology, wildlife management/conservation, and environmental science) clearly had the largest relative size (**Table 1**). Biology/ecology/zoology had a relative size of 53.3%, wildlife management/conservation had a relative size of 36.0%, and environmental science had a relative size of 33.3%, respectively. Comparatively, social-science and humanities-based disciplines were underrepresented (**Table 1**). For example, social sciences, political science/policy, philosophy, anthropology, and geography each yielded a relative size of <4.0% (**Table 1**). Overall, we found that less than a quarter ($I^2 = 22.7$) of human-lion conflict papers had co-authors that derived from two or more disciplines and even fewer ($I^3 = 10.7$) had co-authors from three disciplines. Calculation of an interdisciplinary index ($M^{0.05} = 3$), revealed that this interdisciplinarity occurred between and among co-authors from biology/ecology/zoology, wildlife management/conservation, and environmental science, three inter-related STEM fields.

Co-authors conducting human-lion conflict research were affiliated with four primary types of institutions (academic, NGOs, governments, or private foundations/industries). Those from academic institutions were the most common co-authors of human-lion conflict research, occurring in 86.0% (relative size) of all papers. Co-authors from NGOs were the second-most common (occurring in 28.0% of all papers), followed by co-authors from governments (21.0%), and finally those from private foundations/industries (4.0%). Collaboration of co-authors across these institutional groups was also not uncommon but only tended to involve authors from two or more of these groups (${I_I}^2 = 34.7$) and very rarely from three or more of these groups (${I_I}^3 = 5.3$). The most frequent collaboration occurred among co-authors from academic institutions and NGOs. This type of collaboration was observed in 13.3% of all papers.

We also found that co-authors of human-lion conflict research had affiliations with institutions based in North America, Europe, Africa, and Asia. Co-authors with affiliations in Africa were most common (occurring in 54.7% of all papers) followed closely by co-authors in Europe (46.7%) and in North America (45.3%).

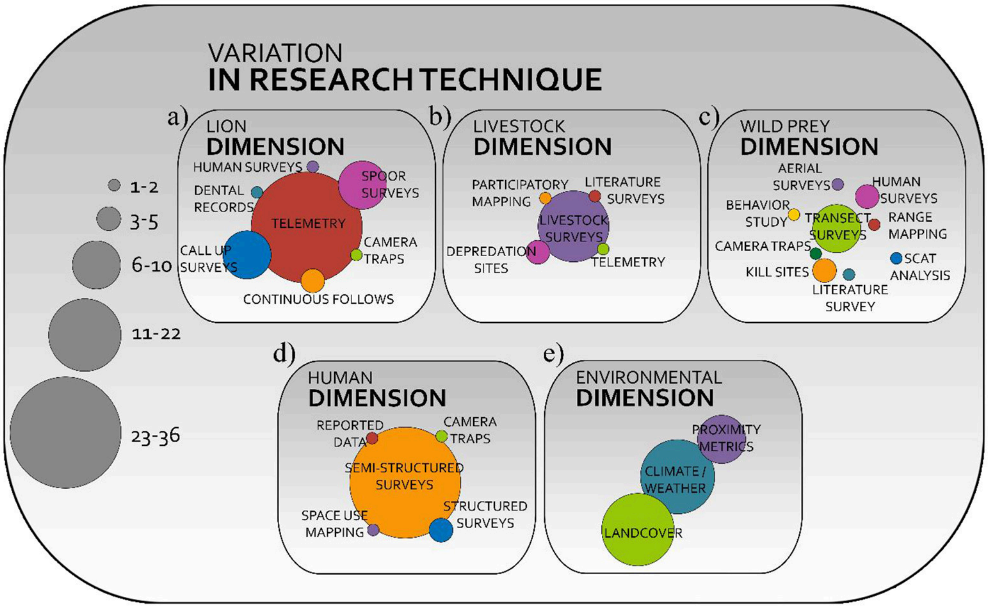

FIGURE 5 | Evident variation in the research techniques used to evaluate the different dimensions associated with human-lion conflict research as inferred from papers published between 1990 and 2015. The size of the circle refers to the number of times each technique was applied across all papers examined.

Co-authors from Asia occurred in just 6.7% of all papers. Our geographic collaboration index indicated that 45.3% of papers were published by co-authors from two or more geographic regions. These geographic collaborations tended to occur most frequently between Europe and Africa, comprising ∼23% of all papers.

Finally, with respect to our keyword analysis, there were 21 papers that we excluded from this assessment given that they did not provide keywords. The number of keywords per paper ranged from four to 10 and averaged 5.98 (se = 0.22). The most frequently used keyword was "lion" followed by "human-wildlife conflict," "*Panthera leo*," "African lion," and "livestock depredation" (Figure S2).

DISCUSSION

Research on human-lion conflict and corresponding coverage of this issue in the popular literature experienced near-exponential growth from 1990 to 2015. The vast majority (89%) of the papers were published across a 10-year period from 2006 to 2015. For instance, there were more papers published per year in 2013, 2014, and 2015 on human-lion conflict than the total number of papers published from 1990 to 2006 (**Figure 2A**). Despite the growth in the research area and the coverage of that research in the popular literature (**Figure 2B**), the global lion population has continued to decline (**Figure 2C**). This questions whether the research relating to human-lion conflict is effectual at conserving lions. We do highlight that scientific research is often reactive (Groves et al., 2002) and thereby, we should anticipate lag effects between publication of research papers and the potential conservation benefits on the species of interest (e.g., Brooks et al., 1999). Thus, given the intensity of human-carnivore conflict research in recent years, it is likely still too soon to see the impacts of that research on the recovery of lion populations.

But the trends that we present here are also part of a broader discussion relating to the divide between human-carnivore conflict research and policy formation (see Macdonald et al., 2010, 2015). Just 2.7% of the papers had co-authors affiliated with units in the political science/policy discipline. Of course, it is not only the policies themselves that are important, but the adoption and implementation of management action at a local level. That point brings us back to the human communities bordering the protected areas where lions typically reside. Lion researchers have made great strides in centering the development of conflict solutions in these communities (e.g., Woodroffe et al., 2007; Hazzah et al., 2014; Loveridge et al., 2017). Thus, co-authors of human-lion conflict research may focus on implementing management strategies deriving from their research rather than endeavoring to inform policy. Moving forward, we suggest that more robust incorporation of experts from political science and policy (see Macdonald et al., 2010; Posner et al., 2016) and adaptive co-management among teams of interdisciplinary researchers and human communities (Berkes, 2004) will be necessary to position conservation efforts into practice (Groves et al., 2002; Redpath et al., 2013). Recent movements (e.g., the Oxford Format) have made efforts to do just that by convening experts from within and, importantly, beyond, the fields of biology/ecology/zoology, wildlife management/conservation, and environmental science to develop new lion conservation approaches (Macdonald and Chapron, 2017).

We found that East Africa (namely Tanzania and Kenya) was the center of human-lion conflict research (**Figure 3**). This is important because East Africa is home to the majority of remaining lions on the planet and four of the reported 10 last stronghold lion populations (those that inhabit protected areas and have >500 adult lions; Riggio et al., 2013; Bauer et al., 2015). Recent projections suggest that lions in East Africa may further reduce by 50% over the next 20 years (Bauer et al., 2015). This decline, along with predictions for Western-Central Africa, could position the species itself on the precipice of extinction throughout much of its range (Henschel et al., 2014; Bauer et al., 2015). Though spatial variation is evident, lion populations are primarily growing in highly-managed, often fenced, reserves in four southern African countries (Namibia, Botswana, South Africa, and Zimbabwe; Bauer et al., 2015; Riggio et al., 2015). There are additional elements at play, apart from fencing, including management philosophy, financial budgets and allocations to conservation efforts, prey abundance, and human population density. But the association between lion population growth and fencing has encouraged an avid debate about the role that fenced parks may plan in the conservation of lions in the future (Creel et al., 2013; Packer et al., 2013; Watson, 2013; Pfeifer et al., 2014; Durant et al., 2015). Importantly, these discussions will need to be informed not only by insights from STEM fields but also by perspectives from the humanities and social sciences (e.g., human perceptions, behaviors, ethics, historic cultures and practices, future goals, and governance structures).

Little Evidence of Interdisciplinarity

Despite the rapid expansion in published human-lion conflict research and calls among the scientific community and funding entities for interdisciplinary research, the number of co-authors on resultant papers has changed little over time (**Figure 2D**). On average, there were 3.28 (se = 0.19) co-authors on any given human-lion conflict paper. A vast majority (86% relative size) of these papers featured co-authors with academic affiliations. Where co-authors of the same paper came from different institutions, the most common collaboration occurred between academicians and researchers from NGOs. Interestingly, the co-authors of human-lion conflict research predominantly derived from three STEM disciplines (biology/ecology/zoology, wildlife management/conservation, and environmental science). These three fields were the most highly related disciplines among the nine represented in our study (**Table 1**). Humanities and social-science disciplines, on the other hand, were greatly underrepresented in human-lion conflict research. Despite these results, we found that the most commonly-evaluated dimension in human-lion conflict research was the human dimension. This might suggest that researchers studying the human dimensions of human-lion conflict research were not disciplinary experts in the social sciences. We caution however, that the relative sizes presented here (**Table 1**) should be viewed as conservative estimates. There is limited information that can be garnered from interpretation of co-author affiliations. Thus, we suspect that there were instances in which a co-author's disciplinary affiliation was not descriptive of that individual's expertise (e.g., a human dimensions expert that currently works as an academic in a Department of Zoology). Furthermore, we highlight the possibility that certain co-authors may have become competent in human-dimensions research without explicit disciplinary training (i.e., self-taught, short courses, and workshops). Nevertheless, given the obvious importance of human dimensions in human-lion conflict research, the low levels of integration of co-authors from fields such as philosophy, anthropology, and social science is troubling.

This point raises the concern that current research on human-lion conflict is unlikely to reflect genuine interdisciplinarity, which requires authentic integration of multiple disciplinary perspectives (Eigenbrode et al., 2007). Different disciplines emphasize distinct questions and ways of framing complex problems (Miller et al., 2008; Elliott, 2017). Conservation problems are almost always importantly complex, requiring multidimensional, rather than singular, solutions (Blaustein and Kiesecker, 2002; Hirsch et al., 2011). One of the major benefits of interdisciplinary research is that it brings these distinct approaches together to generate more comprehensive appreciations of complex problems (Daily and Ehrlich, 1999; Rhoten and Parker, 2004; Chapman et al., 2015). Unfortunately, even if research on human-lion conflict incorporates some co-authors with the ability to use methods from the social sciences, this research is unlikely to reflect a rich, interdisciplinary appreciation of the issues at play if it continues to originate primarily from STEM-dominated disciplinary questions and perspectives. In that case, robust solutions for human-lion conflict will continue to be elusive, problematizing efforts to conserve lions and improve human well-being. Furthermore, given the current disconnect between human-lion conflict research and policy formation, it seems particularly important to encourage research driven by perspectives from policy-oriented disciplines (i.e., Macdonald and Chapron, 2017).

These potential shortcomings however, are not exclusively attributable to lion biologists, zoologists, or ecologists. Lion researchers have made efforts to incorporate experts from the social sciences for many years (see Macdonald et al., 2007) and have, at times, found it challenging to get meaningful collaboration from social scientists and humanities experts (Macdonald et al., 2010, 2013). Thus, the burden of proof in interdisciplinary research falls upon the co-authors from each of the representative disciplinary domains (Campbell, 2005). We do see positive indications that research teams evaluating lion conservation problems are becoming increasingly interdisciplinary (Pooley, 2016; Macdonald and Chapron, 2017) and we expect that to be a trend that will only grow moving forward. Furthermore, the results that we present here should not be particularly surprising. Educational and career training systems are increasingly specialized and tend not to incentivize the development of broad interdisciplinary expertise (Dickman, 2010; Macdonald et al., 2013). This point presents the context for the relatively low levels of interdisciplinarity that we detected within human-lion conflict research and further emphasizes the need for robust interdisciplinary collaboration.

TABLE 1 | Discipline categories for co-authors of human-lion conflict research papers published between 1990 and 2015.

DISCIPLINARY CATEGORIES OF CO-AUTHORS

ABBREVIATION	DISCIPLINE	RELATIVE SIZE
B	BIOLOGY, ECOLOGY, ZOOLOGY	53.3
W	WILDLIFE MANAGEMENT / CONSERVATION	36.0
E	ENVIRONMENTAL SCIENCE	33.3
SS	SOCIAL SCIENCES	4.0
PS	POLITICAL SCIENCE / POLICY	2.7
P	PHILOSOPHY	2.7
A	ANTHROPOLOGY	2.7
S	STATISTICS	1.3
G	GEOGRAPHY	1.3

The relative size of the total co-authorship group presented by each discipline is also presented.

Limited Comparability of Research

While the human dimension (52%) was most commonly assessed, the lion dimension (48%) was a close second. Increasingly, human-wildlife conflict research is as much, or more, about people than wildlife (Treves et al., 2009; Redpath et al., 2010; White and Ward, 2010). Thereby, research on human-wildlife conflict has largely been envisaged as having two predominant spheres (involving humans and wildlife; Manfredo and Dayer, 2004; Redpath et al., 2004; Thirgood and Redpath, 2008) and our results reflect that central tendency. Subsequent expansion of this ideology has reframed these spheres into three domains represented by organisms, habitat, and humans (Decker et al., 2012). We found human-lion conflict research to have five dimensions. Following the human and lion dimensions, the environmental dimension (43%) and the livestock dimension (38%) were the next most-evaluated. The wild-prey dimension was comparatively understudied (27%). This result is interesting given that wild-prey depletion has been presented as a potential causal mechanism associated with lions switching from wild-prey to domestic livestock fueling human-lion conflict (Patterson et al., 2004; Gusset et al., 2009). Furthermore, loss of wild-prey species is one of the biggest concerns for lion conservation in future given that while there might be enough protected land to support lion populations, the utility of that land would be modest without adequate prey to support lion populations (Macdonald, 2016; Wolf and Ripple, 2016). We recommend that efforts be made to increase research on the role of wild-prey in human-lion conflict and carnivore conservation, more broadly (see Wolf and Ripple, 2016).

Research across these different dimensions also showed a pattern of considerable variation in the methodological technique deployed (**Figure 5**). This was particularly evident in the wild-prey dimension where dramatic variation in the style of research should be expected to complicate efforts to compare results across studies, countries, and regions. Such variation is problematic in a number of different disciplines including predator-prey research (Lima and Dill, 1990; Weissburg et al., 2014), but is particularly obvious in research occurring in carnivore-ungulate systems (Moll et al., 2017). An area of potentially productive future research would be a social network analysis (see Nita et al., 2016; Rozylowicz et al., 2017) of the interconnectedness of these prides of lion researchers. The application of social network analysis tools could, for instance, document existing webs of collaboration, chart the spread of research techniques throughout these networks, and identify those portions of the network that disproportionately contribute to research on human-lion conflict.

A New Pride of Lion Researchers

Human-lion conflict research has been much-needed, ground breaking (in many cases), and well-intentioned. However, we have pointed out areas where this research effort can be strengthened. Examination of these areas facilitates an opportunity to synthesize existing information and codify a path forward. Thus, based on this review, we suggest that there is productive space available for the evolution of new prides of lion researchers to examine the different dimensions of human-lion conflict in a way that may be more forward-thinking and effective. Here we relay a series of specific recommendations deriving from our research effort. First, we recommend that researchers endeavor to simultaneously evaluate all five dimensions of human-lion conflict. Whereas it may be possible to partition particular dimensions of human-lion conflict among some research efforts, studying this problem in a holistic manner is necessary to document the factors that account for the most variation observed in spatio-temporal patterns of conflict, for instance. Such evidence is much-needed to prioritize interventionist activities capable of reducing that conflict (Treves et al., 2004; Atwood and Breck, 2012). Second, we recommend that researchers conduct interdisciplinary research (Pooley, 2016) involving full and meaningful integration of contributors from diverse backgrounds, expertise, and affiliations who can bring together multiple disciplinary methods and framings of the problem (Eigenbrode et al., 2007; Miller et al., 2008; Macdonald and Chapron, 2017). Of particular need in human-lion conflict research is the incorporation of experts from the social sciences and humanities. Third, we recommend that researchers increase efforts to study the wild prey dimension. While this dimension was most understudied in our assessment there is good reason to believe that factors associated with wild-prey (e.g., depletion, ecology, movement) are particularly relevant to conflict between people and lions. Thus, increasing research on this topic should improve efforts to conserve lion populations while preserving human interests. Fourth, we recommend that, as much as is possible, researchers assess the different dimensions of human-lion conflict using comparable research techniques. This step would facilitate robust comparisons across studies which could lead to conservation actions that are applicable at broader, more regional scales. Finally, we recommend that research on human-lion conflict continue to make efforts to inform policy actions. Promoting more genuinely interdisciplinary research that is driven by scholars from fields like anthropology, sociology, law, and public policy is likely to help address the research-policy divide. Both the development and enactment of progressive policies will be necessary to sustain species such as lions while preserving the well-being of people in an increasingly anthropocentric world.

AUTHOR CONTRIBUTIONS

RAM was the project leader and contributed to every aspect of the study. KE, MH, SG, JM, SR, BK, DK, RJM, TM, AM, LA, JB, CH, CB, and DM reviewed literature returned from this review, wrote sections of the manuscript and edited the entire manuscript. ET lead efforts to access all of the literature comprising this review and wrote and edited section of the manuscript. All authors equitably contributed to the creation of this review and approve submission to Frontiers.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00049/full#supplementary-material

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How Moments Become Movements: Shared Outrage, Group Cohesion, and the Lion That Went Viral

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Can moments of viral media activity transform into enduring activist movements? The killing of Cecil the lion by a trophy hunter in Zimbabwe in 2015 attracted global attention and generated enduring conservation activism in the form of monetary donations to the research unit that was studying him (WildCRU). Utilizing a longitudinal survey design, we found that intensely dysphoric reactions to Cecil's death triggered especially strong social cohesion (i.e., "identity fusion") amongst donors. Over a 6-month period, identity fusion to WildCRU increased amongst donors. In addition, in line with an emerging psychological model of the experiential antecedents of identity fusion, cohesion amongst donors increased most for those who continued to reflect deeply on Cecil's death and felt his death to be a central event in their own lives. Our results highlight the profound capabilities of humans to commit resources to supporting others who are distant in space and time, unrelated culturally or biologically, and even (as in this case) belonging to another species altogether. In addition, our findings add to recent interdisciplinary work uncovering the precise social mechanisms by which intense group cohesion develops.

Keywords: conservation, activism, groups, identity fusion, prosociality

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INTRODUCTION

Cecil the lion's death in 2015 at the hands of a trophy hunter prompted one of the largest reactions in wildlife conservation history (Macdonald et al., 2016a). Global attention to Cecil's story quickly generated over $1 million in donations, from thousands of individual donors, to the Wildlife Conservation Research Unit (WildCRU), the Oxford University group studying Cecil at the time. Past analyses of the Cecil case and others like it have focused on the factors that trigger a viral media response (Berger and Milkman, 2012; Macdonald et al., 2016a). Considering the dire state of lion conservation (Bauer et al., 2015), Macdonald and colleagues asked whether the "Cecil Moment" presaged a significant shift in commitment to lion conservation: a "Cecil Movement"—a metaphor for a world view in which humanity places a higher value on, and therefore conserves better, not just lions, but wildlife, nature and the wider environment (Macdonald et al., 2016a). Here, we examine this shift empirically.

Our examination is guided by recent work on the social psychology of pro-group commitment. Accumulating studies show that numerous forms of prosociality, including sacrificing one's life for others, are motivated by a particularly lasting form of social cohesion termed "identity fusion" (Swann et al., 2009; Buhrmester and Swann, 2015). People who are strongly fused to a group (e.g., a nation or religion) subjectively experience a visceral sense of oneness with that group, and view fellow members as kin (Buhrmester et al., 2015). For fused persons, personally costly acts that benefit the group can be seen as a moral duty (Swann et al., 2014), compelling them, for instance, to defend their brother-in-arms on the battlefield (Whitehouse et al., 2014) or to donate to victims of terrorist attacks (Buhrmester et al., 2015). Identity fusion thus connotes an unusually affective and personal form of cohesion that is distinct from more cognitive forms of cohesion based on self and group categorization processes (Tajfel and Turner, 1979). Building on these studies, we sought to examine levels of identity fusion in relation to Cecil as well as WildCRU, as well as relationships to pro-social outcomes related to wildlife conservation.

Given that strong fusion promotes such a range of pro-social outcomes in various contexts, we also sought to ask what fosters fusion in the first place? Emerging evidence from anthropological and psychological studies suggests that particular kinds of shared group experiences are especially likely to cultivate identity fusion (see Buhrmester and Swann, 2015 for a review). Specifically, shared experiences that are infrequent and intensely dysphoric, such as painful or shocking group initiation rituals, tend to produce tight social bonds in many contexts and cultures (Whitehouse and Lanman, 2014). Such bonds may arise because these experiences trigger a process of personal reflection and meaning-making that enjoins one's personal identity to that of the group (Swann et al., 2012; Jong et al., 2015). Did these mechanisms of change in fusion occur for those following Cecil's story?

Cecil's story was both ordinary and extraordinary. As another instance of trophy hunting of a large predator, Cecil's story was not especially out of the ordinary (Macdonald et al., 2016a; and for further discussion of perspectives on trophy hunting relating to Cecil, see Di Minin et al., 2016; Macdonald et al., 2016b). Numbers of many large predators, including lions, are declining globally, in part due to trophy hunting (Loveridge et al., 2016). However, the viral spread of Cecil's story through the media as a singular, shocking moment shared by millions globally was extraordinary for at least a moment—relatively few stories of trophy hunting become global media headlines (Macdonald et al., 2016a). But could Cecil's story—a story that had no measurable material impact on the personal lives of donors, most of whom live half a world away in the U.S.—have had lasting changes in identity and motivation to champion conservationist causes? To examine these issues, we sought to test the following hypotheses.

Hypothesis 1: In line with Whitehouse's model of the experiential causes of increased identity fusion (Whitehouse and Lanman, 2014), we hypothesized that participants who experienced high levels of dysphoria in response to Cecil's death would (1) experience strong fusion to Cecil, and (2) in turn, feeling that Cecil's death has bound WildCRU members closer together, experience strong fusion to WildCRU (Swann et al., 2012).

Hypothesis 2: According to theory (Swann et al., 2012; Whitehouse and Lanman, 2014), lasting changes in fusion to a group (e.g., WildCRU) take weeks to months to develop following a precipitating event. Insofar as Cecil's death served as an intensely dysphoric experience, in line with Whitehouse's model, we hypothesized that mean levels of fusion amongst donors to WildCRU would increase over time.

Hypothesis 3: Why might fusion to WildCRU increase over time? Past work suggests that intensely dysphoric, shared experiences promote continued ingroup discussion and reflection on the meaning of the event (Whitehouse, 1996, 2002; Jong et al., 2015). For some, continued reflection may foster the perception that the event was meaningful to one's personal identity and the identities of others who experienced the event similarly (Whitehouse and Lanman, 2014). Thus, we hypothesized that felt levels of dysphoria in the wake of Cecil's death would promote continued reflection and a sense that the event was central to the identities of oneself and other WildCRU donors. Furthermore, we hypothesized that fusion would increase most for participants who both (1) reported especially high amounts of reflection after Cecil's death, and (2) reported especially strong perceptions that Cecil's death has been a central experience for understanding one's personal identity and the identities of others who also experienced Cecil's death.

Hypothesis 4: Understanding the psychological mechanisms underlying what causes fusion to increase is important because strong fusion to a group motivates pro-group actions and attitudes (Buhrmester et al., 2015). We hypothesized that strongly fused WildCRU supporters would be especially engaged in continuing conservation efforts in various ways, such as continuing to donate to WildCRU, perceive wildlife to have significant inherent value, and to be especially social engaged with ongoing conservation efforts worldwide.

METHODS

Participants

After the killing of Cecil the lion, thousands of people globally made donations to WildCRU and were sent occasional e-mail updates about the activities of the conservation organization, especially as it related to Cecil. In an e-mail update sent out in winter 2015, donors were invited to participate in a brief survey about their experiences learning about Cecil and could click on a link taking them to our survey. Participation was purely voluntary and no compensation was offered.

A total of 992 donor participants completed the survey at Time 1. Given the unexpectedly high number of responses, we decided to send out a second survey in the summer of 2016 (Time 2) to test additional hypotheses. All data were analyzed only after Time 2 data collection was completed. The survey was advertised similarly to Time 1 (i.e., at the end of an e-mail update to donors), and participation was again voluntary. There were 563 responses at Time 2, and 160 of those had also completed the Time 1 survey.

The 160 donors who participated in both surveys are the subject of this analysis. Most of the participants resided in the U.S. (89%), were female (83%), college graduates (80%), and worked full time (58%), with a mean age of 53.7 ($SD = 12.02$). Media saturation was especially high in North America, in large part due to coverage by the American television show *Jimmy Kimmel Live* (Macdonald et al., 2016a). Our participant demographics are consistent, at least in terms of country of residence, with viewers of the show. For an in-depth dissection of the role of the media in relation to Cecil's story, see Macdonald et al. (2016a). When asked about their donation frequency (see Supplementary Materials for survey details), 20% of participants reported that they had donated "very frequently to conservation organizations," 31% "regularly," 34% "only on occasion," and 15% that their donation to WildCRU was their first to a conservation fund. All participants provided informed, written consent prior to the Time 1 survey.

Measures

Participants completed the following scales.

State Dysphoria

At Time 1, participants reported state *dysphoria* in reaction to Cecil's death via an 8-item checklist ($M = 4.12$, $SD = 1.76$, $\alpha = 0.63$; scale range 0–8). The checklist asked participants to check whether they had, for instance, felt intense anger in the wake of Cecil's death.

Identity Fusion

At Time 1 and 2, participants also completed the pictorial identity fusion scales (Swann et al., 2009). The pictorial identity fusion scale asks respondents to choose which of five pictorial representations of "self" and "other" best reflect their relationship (Swann et al., 2009). The self and other are represented by two circles in five Venn-diagram options ranging from totally non-overlapping circles to totally overlapping. Participants completed the scales at each time point, once in reference to "Cecil the Lion" as the other target (Time 1: $M = 3.59$, $SD = 1.23$, Time 2: $M = 3.64$, $SD = 1.12$), and again in reference to "WildCRU" (Time 1: $M = 3.05$, $SD = 1.03$, Time 2: $M = 3.26$, $SD = 1.03$).

Depth of Reflection

At Time 2, participants also completed a four-item measure designed to assess their *depth of reflection* on Cecil's death (e.g., "When you reflect on this experience, to what extent does it come to mind in words or pictures as a coherent episode?," $\alpha = 0.61$, $M = 2.31$, $SD = 0.80$). These items were derived from Jong et al.'s (2015) operationalization of depth of reflection following a precipitating event.

Self/Group Centrality

At Time 2, we included a two-question measure designed to assess *self/group centrality*, i.e., the extent to which Cecil's death and story was a personally central experience as well as a similarly central experience for fellow conservationists ($\alpha = 0.63$, $M = 2.78$, $SD = 0.81$). These items were derived from items developed by Newson et al. (2016) to assess the how central an event was perceived to be to one's personal identity.

Pro-group Outcomes

At Time 2, we additionally asked participants (1) whether they had donated again to WildCRU in the previous months (38% had done so), (2) two questions to measure the extent to which they felt that the lives of lions and all wildlife were invaluable ($\alpha = 0.91$, $M = 4.13$, $SD = 0.99$), and (3) five questions to measure how engaged they had recently been in wildlife conservation efforts (e.g., "do you feel your thoughts about politicians and voting are now more influenced by wildlife conservation issues?," ($\alpha = 0.71$, $M = 2.95$, $SD = 0.63$). Note: Examinations of distribution normality of key variables (e.g., Q-Q plots, histograms) suggested the use of parametric tests.

RESULTS

We followed the steps of statistical mediation (Hayes, 2013) to test Hypothesis 1 (i.e., that dysphoric reactions to Cecil's death generated fusion to Cecil, and in turn, fusion to fellow WildCRU supporters). In a first regression, represented by the "a path" in **Figure 1**, dysphoric intensity predicted fusion to Cecil, standardized regression coefficient, $\beta = 0.27$, $t_{(157)} = 3.45$, $p < 0.01$. In a second regression, represented by the "c path" in Figure 1, dysphoric intensity predicted fusion to WildCRU, $\beta = 0.23$, $t_{(154)} = 2.90$, $p < 0.01$. Then, in a third regression with dysphoric intensity and fusion to Cecil entered as simultaneous predictors of fusion to WildCRU, the effect of intensity on fusion to WildCRU, the c' path, was no longer statistically significant, $\beta = 0.05$, $t_{(153)} = 0.78$, $p = 0.45$, while the effect of fusion to Cecil on fusion to WildCRU remained significant, $\beta = 0.62$, $t_{(153)} = 9.41$, $p < 0.01$, with Sobel $z = 3.46$, $p < 0.01$, indicating the presence of statistical mediation. These results supported Hypothesis 1.

We turned next to assessing Hypothesis 2 (i.e., that fusion to WildCRU would increase from Time 1 to Time 2). In line with our hypothesis, a paired *t*-test revealed that fusion to WildCRU increased overall (Time 1 $M = 3.05$, $SD = 1.03$ vs. Time 2 $M = 3.26$, $SD = 1.03$), $t_{(153)} = 2.41$, $p < 0.02$. To our knowledge, this finding represents the first empirical demonstration of a longitudinal overall increase in fusion with a group resulting from a single precipitating event (in this case, the death of Cecil). This finding is unique given the remarkable stability of fusion that has been reported in response to other types of significant group events (Vázquez et al., 2017). We also examined via a paired *t*-test whether fusion to Cecil changed over time and found no change ($M = 3.59$, $SD = 1.23$) to Time 2 ($M = 3.64$, $SD = 1.12$), $t_{(153)} = -0.54$, $p = 0.59$).

To examine Hypothesis 3, we first examined whether levels of dysphoric intensity reported at Time 1 predicted reported levels of reflection and self/group centrality measured at Time 2. We conducted two linear regressions, and found that Time 1 dysphoric intensity predicted both depth of reflection, $\beta = 0.24$, $t_{(158)} = 3.05$, $p < 0.01$, and self/group centrality $\beta = 0.25$, $t_{(158)} = 3.24$, $p < 0.01$ at Time 2. In line with Hypothesis 3, these results suggest that high levels of shock following Cecil's death tended to promote deep reflection and a sense that the event was central to the identities of oneself and other WildCRU members.

We next examined whether fusion increased most for participants who both (1) reported especially high amounts of reflection after Cecil's death, and (2) reported especially strong perceptions that Cecil's death has been a central experience

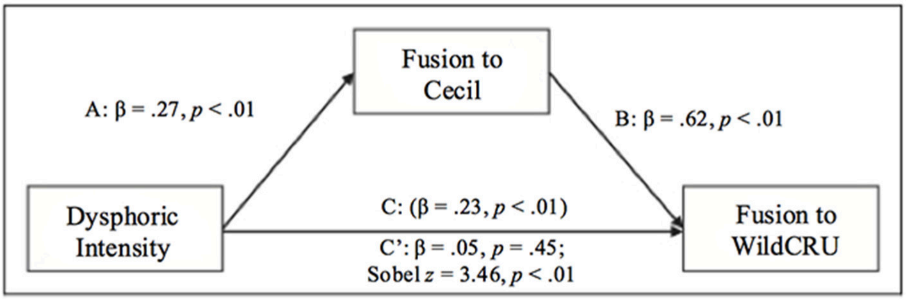

FIGURE 1 | Mediation model showing the effect of dysphoria on fusion to WildCRU was mediated by fusion to Cecil.

TABLE 1 | Effects of fusion to WildCRU on pro-social outcomes.

Pro-social Outcome	Model summary statistics (fusion to WildCRU as predictor)
Continued to donate to WildCRU	*Logistic regression:* $b = 0.41$, $SE = 0.17$, Wald $X^2_{(1)} = 5.84$, $p < 0.01$, $OR = 1.50$.
Perceived value of wildlife	*Linear regression:* $\beta = 0.24$, $t_{(158)} = 3.16$, $p < 0.01$
Conservation engagement	*Linear regression:* $\beta = 0.31$, $t_{(158)} = 4.06$, $p < 0.01$

for understanding one's personal identity and the identities of others who also experienced Cecil's death. To test this, we conducted a multiple regression with reflection, centrality, and their interaction as predictors of donors' change in fusion to WildCRU from Time 1 to 2. The analysis revealed a significant interactive effect of reflection and centrality on fusion change, $\beta = 0.21$, $t_{(150)} = 2.78$, $p < 0.01$ (see **Figure 2**). The conditional effect of reflection on fusion change was significant only when centrality was high [i.e., +1 SD), $\beta = 0.35$, $t_{(150)} = 3.14$, $p < 0.01$, but not low (i.e., –1 SD), $\beta = -0.08$, $t_{(150)} = -0.67$, *n.s.*, indicating that increases in fusion to WildCRU occurred for participants who engaged in high levels of reflection and also felt that Cecil's death was a central self and group experience, whereas participants who did not score highly on both the reflection and centrality measures reported little to no change or a decrease in fusion.

Finally, we examined Hypothesis 4 via a series of regressions (see **Table 1** summary). In a logistic regression, mean fusion to WildCRU combined across both times predicted whether participants had made another donation to WildCRU beyond their initial donation [$\beta = 0.41$, $SE = 0.17$, Wald $X^2{}_{(1)} = 5.84$, $p < 0.02$, Odds Ratio = 1.50]. In two linear regressions, fusion to WildCRU also predicted perceptions of wildlife value [$\beta = 0.24$, $t_{(158)} = 3.16$, $p < 0.01$], and conservation engagement [$\beta = 0.31$, $t_{(158)} = 4.06$, $p < 0.01$]. Consistent with Hypothesis 4, these results demonstrate that strongly fused WildCRU supporters were especially engaged, continuing conservation efforts in ways that constitute a sustainable movement.

Given that of those who completed Wave 1 ($N = 992$), $N = 160$ completed Wave 2 (16.1% of the Wave 1 total), we also examined whether attrition was random or systematic. First, we examined whether Wave 1 participants who did not complete Wave 2 differed from those who completed both waves on demographic and key study variables. The two samples did not differ in terms of gender, *Chi-square* (1) = 0.11, $p = 0.74$; education, $t_{(975)} = 1.05$, $p = 0.30$; occupation status, *Chi-square* (1) = 0.27, $p = 0.60$; age, $t_{(956)} = -1.74$, $p = 0.08$; nor how they learned of Cecil's death, *Chi-square* (3) = 0.99, $p = 0.80$. Slightly more participants who completed both waves reported residing in a country other than the U.S. (11.3%) than participants who only completed Wave 1 (6.3%), Chi-square (1) = 5.01, $p = 0.03$. For the dysphoric reactions scale, participants who completed both waves reported no more dysphoria ($M = 4.12$, $SD = 1.76$) than those who did not participate at Time 2 ($M = 3.97$, $SD = 1.84$), $t_{(990)} = -0.97$, $p = 0.33$. For the fusion scales, participants who completed both waves reported being slightly more fused to WildCRU ($M = 3.05$, $SD = 1.03$) and Cecil ($M = 3.59$, $SD = 1.23$) than those who only completed Wave 1 (WildCRU: $M = 2.83$, $SD = 1.07$; Cecil: $M = 3.28$, $SD = 1.33$), $t_{(971)} = -2.22$, $p = 0.03$, and $t_{(981)} = -2.73$, $p = 0.006$, respectively. It is plausible that those who initially felt a deeper connection with Cecil and WildCRU would be more likely to read the emailed update from WildCRU and notice the survey link at Time 2. Also note that there are small differences in *N*'s and corresponding *df*'s for analyses because we did not eliminate participants' data if there were missing cells.

We also examined the full Time 1 dataset ($N = 992$) to see whether the results reported with the $N = 160$ subset were consistent with each other. We tested the mediation result from Time 1 data involving the dysphoric intensity, fusion to Cecil, and fusion to WildCRU variables. The results were very similar. First, dysphoric intensity predicted fusion to Cecil, standardized regression coefficient, $\beta = 0.27$, $p < 0.01$, and fusion to WildCRU, $\beta = 0.21$, $p < 0.01$. Fusion to Cecil also predicted fusion to WildCRU, $\beta = 0.67$, $p < 0.01$. Then, in a regression with dysphoric intensity and fusion to Cecil entered as simultaneous predictors, the effect of intensity on fusion to WildCRU was in a positive direction but no longer statistically significant, $\beta = 0.03$, $p = 0.25$, while fusion to Cecil remained significant, $\beta = 0.66$, $p < 0.01$, with Sobel $z = 8.04$, $p < 0.01$.

In addition, one likely cause of attrition was that, unlike most studies with longitudinal designs, we offered no material incentive to complete the survey. Another likely cause was

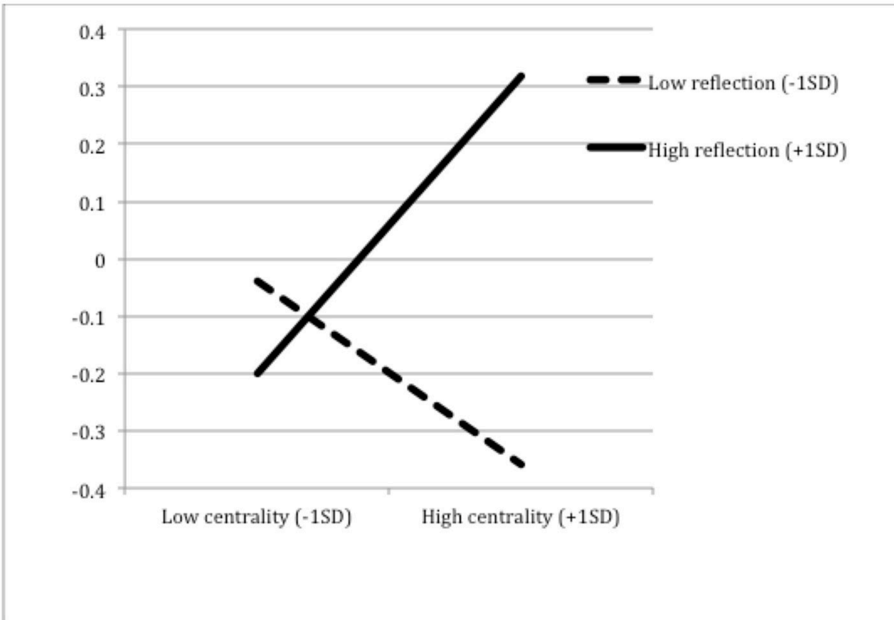

FIGURE 2 | Interactive effect of reflection and centrality on change in fusion to WildCRU from Time 1 to Time 2.

that the survey was advertised toward the end of a long e-mail primarily focusing on updates regarding Cecil's story and WildCRU conservation efforts, thus many readers may have simply not noticed the survey link. Also, given that the total N for those who completed both waves was 160, well exceeding the required sample size to detect a medium effect size in a multiple regression with up to 10 predictors (at power =0.8 and $p < 0.05$), and that there were only minor differences between those who completed only wave 1 and those who completed both waves, we believe that attrition was non-systematic.

DISCUSSION

Overall, our results reveal one possible psychological pathway by which a viral moment can have long-term effects on supporters' identities and behavior. The case of Cecil may seem remarkable in that none of those donating to lion conservation as a consequence were affected personally in any practical or material way by Cecil's death. But this may be true of social movements in human history in general. For instance, many supporters of the civil rights movement in the U.S. or hunger strikes in Northern Ireland or, more recently, efforts to bring about regime change during the Arab Spring, have been motivated to get involved despite being far removed from their seminal events, perhaps even on the other side of the world. Indeed, the Arab Spring and other revolutionary movements have benefitted from diaspora communities in other parts of the world providing crucial diplomatic and financial support (Moss, 2016). If we better understand the psychology involved in generating identity fusion to groups involved in social movements, and in particular the role of unique, dysphoric, transformative experiences in augmenting group cohesion, we can begin to explain the failures and successes of specific moments in history to generate enduring movements, even from a great distance. We can also harness these processes to help solve collective action problems of other kinds, not only in domains like conservation but also closely related global problems such as climate change or antibiotic resistance (Whitehouse, 2014). Conversely, more destructive expressions of the same psychological processes (e.g., foreign fighters who have joined ISIS) may be responded to more effectively if we understand the role of shared dysphoria in motivating extreme pro-group action of all kinds (Whitehouse et al., 2017).

Our investigation of WildCRU donors has been guided by a larger collaboration that aims to leverage behavioral insights from multiple disciplines in order to create and sustain high levels of human cooperation in contexts where it is desperately needed (e.g., wildlife conservation, social and economic conflicts, etc.). Here, we are building on efforts to synthesize two bodies of work, one based on Whitehouse's anthropological studies of the experiential causes of social bonding (Whitehouse, 1996; Whitehouse and Lanman, 2014), and the other based on Swann's social psychological studies of the nature and consequences of identity fusion (Swann et al., 2009; Buhrmester and Swann, 2015). This synthesis is highly interdisciplinary, involving collaborations with mathematical modelers (e.g., Salali et al., 2015; Whitehouse et al., 2017), historians (e.g., Whitehouse et al., 2015), archaeologists (e.g., Gantley et al., 2018), cultural evolution theorists (e.g., Atkinson and Whitehouse, 2011), and developmental psychologists (Watson-Jones et al., 2014;

Rybanska et al., 2017)—to name only a few of the disciplines contributing to theory building on this topic. Our present study is the first to apply this emerging theoretical synthesis to work in the domain of human dimensions of wildlife conservation. In doing so, we adapted study measures from instruments that have been previously validated as part of the above synthesis (Swann et al., 2009; Jong et al., 2015). Furthermore, our examination extends the synthesis by focusing on a precipitating event (i.e., Cecil's death) that was centered largely on a wild animal. Past studies have focused on events involving only humans (e.g., the Boston Marathon Bombings, Buhrmester et al., 2015), thus our study's findings add to the generalizability of the psychological processes that we have examined.

Our findings point to the need for continued future research along several avenues. More empirical work is needed to examine the extent to which continued reflection after a precipitating event is caused by aspects of the event itself (i.e., its affective intensity, uniqueness, etc.) vs. communication between group members in the wake of the event. Understanding the impact of continued communication, as well as identifying the key components of fusion-augmenting communication after a precipitating event, could lead to positive practical applications. In addition, future work should examine how perceptions of donation usage may impact both continued giving as well as group bonding. In our case, donors learned from WildCRU's newsletter and website that all donations would be used to achieve the organization's strategic plan, a plan that includes the study of the ecology and conservation of lions such as Cecil but is much broader in scope (see https://www.wildcru.org/about-wildcru/2020-vision). The Cecil case thus shows that many individuals are willing to give (sometimes rather large sums) to broad wildlife conservation efforts based on a single, compelling narrative.

Lastly, can our results facilitate Macdonald et al.'s (2016a) vision of "Cecil Moment" blossoming into a "Cecil Movement"? At the very least, our evidence—that depth of reflection and perception of event centrality underlie increases in fusion over time—should cause conservation advocates to ask how these processes can be amplified to increase fusion amongst supporters (and indeed, to create some level of fusion among initial non-supporters). In addition, advocates and researchers alike should seek out ways to reach the millions who for reasons unknown have not felt swayed by viral moments like Cecil's. Is there a hard cap on the number of conservationist hearts to be won, or could all of humanity rally as one?

Our findings, especially those suggesting that Cecil's story sparked sustained support for WildCRU, give us at least some measure of hope that broad swaths of humanity can and do wish to support not just specific animal rights or wildlife causes, but also broader organizations involved in an array of research and conservation activities with a global focus. And in the case of lions, whose numbers have declined, on average, by 43% over the last three leonine generations (Bauer et al., 2016), greater sustained commitment to their conservation by citizens of the range states and of the wider world, cannot come soon enough.

DATA AVAILABILITY

The raw data supporting the conclusions of this manuscript will be made available by the corresponding author, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

This study was conducted in accordance with and approved by the School of Anthropology and Museum of Ethnography Research Ethics Committee at the University of Oxford. All subjects gave written informed consent in accordance with the Declaration of Helsinki.

AUTHOR CONTRIBUTIONS

DM and HW contributed equally as joint senior authors. All authors designed the measures. MB collected and analyzed the data. All authors contributed to and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00054/full#supplementary-material

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Listening to Lions: Animal-Borne Acoustic Sensors Improve Bio-logger Calibration and Behaviour Classification Performance

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Efforts to better understand patterns of animal behaviour have often been restricted by several environmental, human and experimental limitations associated with the collection of animal behavioural data. The introduction of new bio-logging technology has offered an alternative means of recording animal behaviour continuously and is being used in an increasing number of studies. Accurately calibrating these bio-loggers, however, still remains a challenge in many cases. Using lions as an example species, we test how audio recordings from animal-borne acoustic sensors can improve calibration and behaviour classification. Through a collaborative effort between computer scientists, engineers, and zoologists, custom designed acoustic bio-loggers were fitted to eight lions and recorded audio simultaneously with accelerometer and magnetometer data. Audio recordings were then used as the source of ground truth to train random forest classification models as well as to provide additional predictor variables for behaviour classification. We demonstrated near-perfect classification performance for five lion behaviour classes when all component variables were combined, with an average per-class precision of 98.5%. Using accelerometer features only, the audio-trained classifier predicted behaviours with an average per-class precision of 94.3%. On-animal audio recordings are therefore able to provide a valuable source of ground-truth for calibrating bio-loggers while also offering additional predictive features for increasing the accuracy of behaviour classification. This technological innovation has wide ranging application and provides a useful tool for behavioural ecologists wishing to collect fine scale behavioural data for animal research and conservation.

Keywords: African lion, acoustic monitoring, behaviour classification, bio-logger calibration, machine learning, random forest

INTRODUCTION

Remote data logging, also referred to as bio-logging or bio-telemetry, has evolved rapidly with new available technologies. Initially, studies focusing on animal spatial ecology were revolutionised by the introduction of GPS tracking methods in the 1980's which provide accurate and long-term location information at varying resolutions (Rutz and Hays, 2009). More recently, there has been a shift in focus to providing behavioural information in conjunction with location data using similar archival data-loggers in order to better understand the drivers of animal behaviour. To achieve this, a substantial collaborative effort between zoologists, computer scientists, and engineers has been required. The resulting technological advances have transformed the field of behavioural ecology with an increasing number of studies now relying on animal attached sensors to record behaviour (Brown et al., 2013). This rapid transition likely resulted from the need to overcome a number of difficulties associated with direct observation. These difficulties may include biases suffered as a result of observer presence (Caine, 1990; Gutzwiller et al., 1994) or the inability continuously to observe the focal animal if it is an elusive species, or a species that occurs in inaccessible habitats. In addition, direct observations require considerable time and effort on the part of the observer and thus can be heavily influenced by human physical limitations (Cagnacci et al., 2010).

While bio-loggers provide a solution to most of these challenges, they also have several drawbacks of their own. Firstly, the size of such devices may limit their use on smaller animals where it is not feasible to design a unit that weighs <2% of the animal's body mass. This is necessary to prevent behavioural changes and increases in energy expenditure (Cooke et al., 2004). Secondly, in most cases, researchers are still required to spend time in the field observing the study animal in order to calibrate the data generated by the bio-logger. This is commonly done using video cameras held by the observer with subsequent video labelling that can be matched to the corresponding bio-logger data by time stamps (Kawabata et al., 2014; McClune et al., 2014; Lush et al., 2015; Wang et al., 2015). Thirdly, and perhaps a more fundamental problem is that many types of bio-loggers do not achieve desirable results in discerning between behaviours. Recent studies still fail to differentiate accurately between more than three basic activities (Grünewälder et al., 2012; Lush et al., 2015; Wang et al., 2015).

The majority of bio-loggers used in animal behaviour studies generally rely on one or a combination of three microelectromechanical systems (MEMS) sensors: accelerometer, magnetometer and a gyroscope. An accelerometer measures the acceleration forces of the body to which it is attached (Albarbar et al., 2009) while a magnetometer measures magnetic field strength and direction (Herrera-May et al., 2016). Gyroscopes, although not as common, are used to measure angular rate of rotation (Piyabongkarn et al., 2005). In some cases, animal borne video cameras have been included to provide ground truth for directly calibrating accelerometer data but only provide visual validation for short periods due to the high power and data storage requirements for recording video (Watanabe and Takahashi, 2013; Volpov et al., 2015; Pagano et al., 2017). Audio recording can also be used to collect behavioural information as shown by Insley et al. (2008) on fur seals and Lynch et al. (2013) on deers. These studies inferred animal behaviour by visually reviewing spectrographic patterns but did not incorporate any statistical learning for automatic behaviour classification. To our knowledge, the use of audio recordings as a method of calibrating on-board movement sensors as an alternative to video footage and direct observation has not been tested. In this study, we present a novel method for calibrating bio-logger signals using simultaneously captured on-collar audio recordings from a custom designed bio-logger. In so doing, we provide suggested improvements to the issues surrounding bio-logger calibration and behaviour differentiation. We further demonstrate near-perfect (>99%) classification accuracy when we combine audio features with other sensor data, especially for behaviours which are typically misclassified using motion sensors alone (e.g., drinking water). Thus, capturing synchronised audio and multi-sensor data has not only the potential to provide detailed ground-truth, but also provides extremely accurate automatic behaviour classification.

MATERIALS AND METHODS

Study Site

The study took place on the privately-owned Bubye Valley Conservancy (BVC). The BVC is ∼ 3,400 km^2 and is located in the lowveld region of southern Zimbabwe between latitudes 21.209 and 21.851° South, and longitudes 29.798 and 30.521° East. We focused on the south-western section of BVC where an ongoing lion research project has been conducted since 2009. For a full description of the study site see du Preez et al. (2014).

Bio-loggers

Bio-loggers were custom designed through a collaborative research partnership between zoologists, computer scientists, and engineers with the overall objective of developing a device capable of recording lion behaviour continuously and accurately. The loggers were manufactured to attach onto existing lion tracking collars produced by Africa Wildlife Tracking (AWT), Pretoria, South Africa and measured ∼ 50 × 20 × 30 mm with a mass of <150 g (**Figure 1**). Each unit comprised a triaxial accelerometer and magnetometer, with both sensors sampling at 32 Hz per axis and a mono-electret microphone sampling audio at 16 kHz with an 8-bit resolution. The microphone circuit used a compander to provide dynamic gain adjustment where more amplification is made when the ambient audio is quiet. Custom firmware was written for an 8-bit AVR microcontroller which also included a low-power 802.15.4 radio unit which was used for time-synchronising the bio-logger to a base station upon deployment. Data was logged to a 32 gigabyte micro-SD card. The bio-logger was powered by 3 CR123A lithium cells and encased in an epoxy resin reinforced housing, with a hydrophobic vent for the microphone. **Table 1** shows the relative current draw for each particular sensor, including the cost of logging to the SD card. As can be seen, the audio sensor consumes nearly 100 times as much power as the accelerometer, and this is mainly due to the cost of

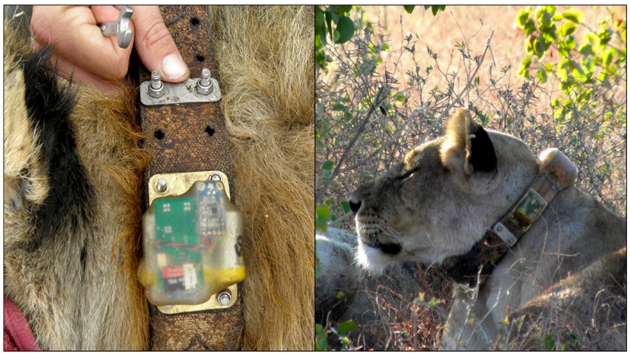

FIGURE 1 | Image showing bio-logger bolted on to the GPS collar fitted to a lioness.

TABLE 1 | Current draw and estimated lifetime using different sensors.

Active Sensor	Total current draw (mA)	Estimated lifetime (days)
Accelerometer only	0.35	535
Magnetometer only	0.50	375
Microphone only	26.0	7

storing the audio data into the SD card, as 16 kilobytes needs to be written per second, compared with 96 bytes per second for the accelerometer or magnetometer.

Ethical Statement

This study was carried out in accordance with the recommendations of the Use of Animals in Research, ASAB/ABS. The protocol was approved by the University of Oxford Animal Welfare and Ethical Review Board and the University Veterinary Services Department. Project staff were qualified to capture and handle the study animals by attendance at Zimbabwe's Physical and Chemical Capture of Wild Animals Course and held valid drugs licenses (Dangerous Drugs License No. 2014/16). The animals were captured with permission from the landowner and conservancy management.

Data Collection

In November 2014, we captured eight lions (five males and three females) that had been previously fitted with standard AWT satellite GPS collars. For a full description of the capture method see du Preez et al. (2015). Once the animals had been immobilized, the bio-loggers were bolted on to the existing GPS collars and started recorded audio (8 bit, 16 kHz mono) and three-dimensional accelerometer and magnetometer data (32 Hz) continuously until the batteries failed between 4 and 10 days later. Lions were recaptured ∼ 1 month after initial capture and the loggers removed for data extraction.

Data Management

In total, 80 predictor variables were calculated from the three accelerometer and magnetometer axes (40 variables for each component) for each 1 s window of data (**Table 2**). Many of the

TABLE 2 | Predictor variables calculated over each second of data, used for RF classification.

Component	Feature	Definition	Number of variables
Accelerometer and magnetometer	Average axes values	Mean for X,Y,Z axes	6
	Variance in each axis	Variance for X,Y,Z axes	6
	Pitch	Ratio between X,Y, and Z axes	2
	Roll	Angle between Y and Z axes	2
	Overall dynamic body acceleration	Sum of the dynamic acceleration values for X,Y, and Z axes	2
	Standard deviation of magnitude	Standard deviation of the square root of the sums of squares of values in X,Y, and Z axes	2
	Fast fourier transformations	Energy level in 8 × 4 Hz frequency bins for each axis	48
	Peak frequencies	Frequency bin with maximum energy level for each axis	6
	Peak amplitudes	Power of frequency bin with maximum energy level for each axis	6
Audio	Mean energy	Mean energy in 24 frequency bands between 20 Hz and 8 KHz using Gabor filter bank	24
	Energy variance	Variance in energy in 24 frequency bands between 20 Hz and 8 KHz using Gabor filter bank	24

predictor features chosen for the movement sensor data have also been used in other studies (Gerencser et al., 2013; Wang et al., 2015). In addition to these features, 48 predictor variables were calculated from the corresponding audio recordings creating a combined feature set of 128 variables (see **Table 2** for a description of each feature). Energy mean and variance were used as audio variables as they represent the zeroth and first order statistical moments of power in the 24 frequency bands as is often used in speech recognition (Kos et al., 2013). The energy mean captures whether a tone is present or not over a window, while energy variance better captures impulsive sounds such as foot falls during running.

For each individual lion, random sections of audio recordings were labelled manually into one of five behavioural states (fast, slow, stationary, eat, and drink) by two lion ecologists with a minimum of 2 years of experience working on lions. We grouped running and trotting together as "fast" behaviour while walking was classed as "slow" behaviour. We were able to distinguish between these two behavioural states by the sound and pace of the lion's footfalls. Eating behaviour was discernible by the sound of chewing and bone crunching along with aggressive vocalisations that are often associated with group feeding. Drinking events were recognized by the sound of lapping water with regular swallowing (Samples of these audio recordings can be found in the **Supplementary Material**). We labelled a total of 20.5 h of audio which was then matched to logger measurements by corresponding time stamps. This resulted in a total labelled dataset of 73930 samples each 1 s long. We randomly subsampled this dataset to 16223 1 s samples by balancing across behavioural state and individual where possible to ensure that each individual and behaviour were sufficiently represented (**Table 3**). Poor representation of certain behavioural classes has been shown to reduce classification performance (Grünewälder et al., 2012). Additionally, class imbalances can result in a bias toward the over-represented classes (Stumpf and Kerle, 2011).

Statistical Learning to Predict Behaviour

We used the Random Forest (RF) classification method developed by Breiman (2001) to infer behaviour from bio-logger measurements. This method is advantageous as it is computationally fast, robust to outliers and noise and also offers variable importance estimates for classification (Breiman, 2001). The analysis was done using the random forest package (Breiman, 2001) in the R statistical program (R Core Team, 2016), within the R studio integrated development environment (R Studio Team, 2016). For all models, we set the number of trees (ntree) to 1,000 and used the recommended value ($\sqrt{Number\ of\ variables}$) for the number of variables considered at each split (mtry) which has been shown to yield optimal performance (Díaz-Uriarte and Alvarez de Andrés, 2006).

We carried out a 5-fold cross-validation to train and test two RF models, one with all component features combined and another with only accelerometer features. We compared the behaviour classification performance of the models using accuracy, precision and recall. Accuracy is a measure of overall model performance and is defined as the proportion of correctly classified data. Precision is defined as the proportion of correctly predicted positive classifications for a particular behavioural state while recall (also called sensitivity) refers to the proportion of data of a particular behavioural state that is classified correctly as positive (Sokolova and Lapalme, 2009; Bidder et al., 2014). We used accuracy as the overall performance metric due to its simplicity and the fact that it takes into account all classification outcomes (Bidder et al., 2014; Wang et al., 2015). To evaluate prediction performance for each behavioural state, we used precision as the main performance metric as it is most applicable to biological inferences which generally rely on true positive classifications, as was the case in this study (Bidder et al., 2014). We included recall as recommended by Bidder et al. (2014) for novel classification methods.

TABLE 3 | Summary of balanced dataset showing number of seconds for each behaviour and individual.

Tag ID	Sex	Drink	Eat	Fast	Slow	Stationary	Total
A1	Female	684	1,021	429	598	515	3,247
A3	Female	196	0	163	598	515	1,472
A4	Male	684	330	227	548	514	2,303
A8	Male	684	1,020	209	597	514	3,024
A9	Male	684	1,020	237	63	514	2,518
A10	Male	0	0	226	598	514	1,338
A11	Male	668	209	332	598	514	2,321
Total		3,600	3,600	1,823	3,600	3,600	16,223

RESULTS

We collected a total of 44 lion-days of useable data from 7 individual lions. One female lion was excluded from the final dataset as the magnetometer malfunctioned from the time of deployment. Our final subsampled dataset consisted of 16,223 data points with an hour of data for each behavioural class except "fast" for which we could only accumulate 1,823 s of data.

Behaviour Classification Performance

Combining all component features resulted in near perfect classification performance with an average per-class precision of 98.5% (**Table 4A**). Drink, fast, slow and stationary behaviours were predicted with ∼99% precision while eating was ∼3% lower with a precision of 96.2%. Training the classifier using accelerometer features only, resulted in an average per class precision of 94.3% (**Table 4B**) with only eating behaviour being predicted with <90% precision.

DISCUSSION

Recording the active behavioural states of African lions such as running, drinking or eating by directly observing study individuals can often be difficult as lions are mostly active at night and can be challenging to follow in areas with thick

TABLE 4A | Confusion matrix of actual (rows) vs. predicted (columns) behaviours for audio, accelerometer, and magnetometer features combined.

Behaviour	Drink	Eat	Fast	Slow	Stationary	Recall (%)	Precision (%)
Drink	3,514	53	0	12	21	97.6	98.8
Eat	21	3,537	14	11	17	98.3	96.2
Fast	0	7	1,814	2	0	99.5	99.2
Slow	5	38	1	3,553	3	98.7	99.2
Stationary	15	40	0	3	3,542	98.4	98.9

TABLE 4B | Confusion matrix of actual (rows) vs. predicted (columns) behaviours for accelerometer features only.

Behaviour	Drink	Eat	Fast	Slow	Stationary	Recall (%)	Precision (%)
Drink	3,433	118	0	5	44	95.4	95.1
Eat	149	3,122	14	170	145	86.7	87.7
Fast	0	5	1,811	6	1	99.3	99.1
Slow	3	221	2	3,371	3	93.6	94.9
Stationary	26	94	0	0	3,480	96.7	94.7

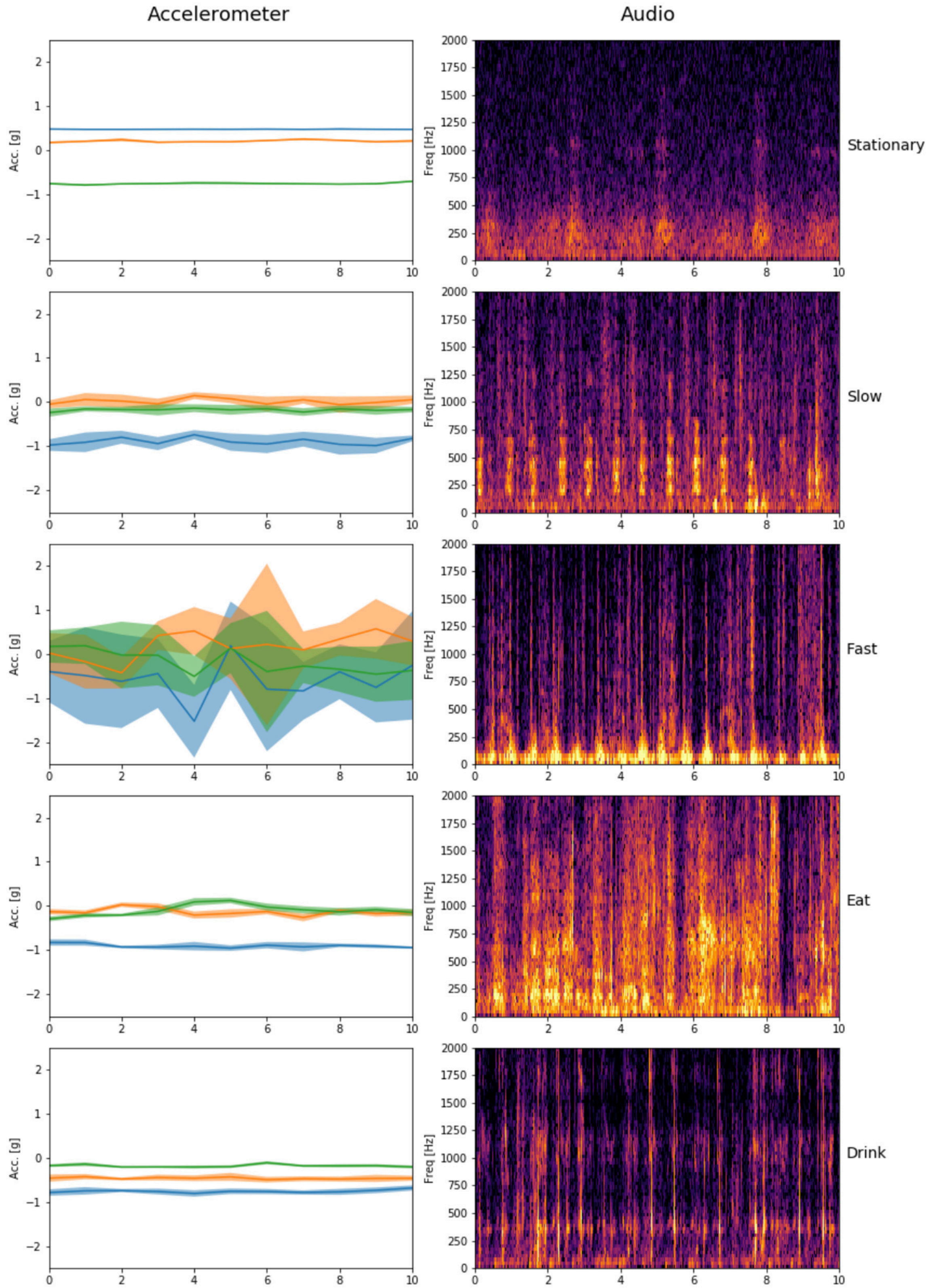

FIGURE 2 | Synchronised accelerometer data and audio spectrograms for each behavioural state. Lines and shaded regions on accelerometer plots represent mean and standard deviation, respectively for each accelerometer axis.

vegetation such as BVC. Adult lions, weighing in excess of 150 kg, are capable of carrying bio-logging devices attached to collars which can offer unique insights into their behavioural patterns. Using custom-designed acoustic bio-loggers, we found that audio can be used as an effective source of ground truth for training accurate behaviour classification models.

Six years ago Grünewälder et al. (2012) suggested that the collection of behavioural observations for calibrating bio-logging devices could be done remotely in the near future. Achieving this objective, however, required the integration of technological and zoological knowledge and skills both for the development and data analysis phases, which was achieved through an interdisciplinary research partnership. Our results indicate that remotely collected audio recordings can be used as a reliable source of ground truth for calibrating bio-loggers by matching audio labels to logger data following logger retrieval and thereby eliminate the need for calibration from direct observations (**Figure 2** illustrates how audio and movement sensor data are synchronised).

It is useful to note that a relatively small number of ground truth labels (1 h per behavioural state) were required to build an accurate classifier, although it is important to ensure that all behavioural classes are sufficiently represented in the training dataset (Grünewälder et al., 2012). This requirement can be fulfilled by continuously logging audio over several days which increases the likelihood of recording rarer behavioural events.

The total of 44 lion-days of audio from 7 individuals provided considerably more data for calibration of rarer behavioural events (eat, drink, and fast) than could have been realistically achieved using video footage recorded by an observer or a video collar. In comparison, Pagano et al. (2017) recorded a total of 140 h of video for accelerometer validation from 5 ice bears fitted with video collars. Although visual determination of animal behavioural states is likely to be more objective than those which are determined audibly from sound recordings, we found that in general, the behaviour of the study animal could be determined easily from certain acoustic cues as outlined in section Data management. Insley et al. (2008) who also made use of an animal-borne acoustic recording device reported being able to clearly differentiate between resting and other active behaviours of northern fur seals. Similarly, Lynch et al. (2013) list in detail, the audible behaviours that could be captured by their animal-borne acoustic devices fitted to wild mule deer. While most behaviours may be clearly discernible using this method, short periods of ambiguous sound signals will likely be recorded and, depending on the objective of the research, may require concurrent observational data collection to confirm the behavioural state (Lynch et al., 2013). In some cases, interference from other sound sources may also make it difficult to determine behaviour. Such interference may result from self-vocalisations, vocalisations emitted by other species, anthropogenic sources (e.g., vehicles) or environmental sources (e.g., wind and rain). The use of this approach should also consider the acoustic characteristics of the species of interest as the behaviour of certain species may not be sufficiently audible, even at close range.

The results from the model built using the different component datasets showed that audio and magnetometers can also be used as additional sensor modalities for classification with high model predictive performance when accelerometer, magnetometer and audio features are combined. However, due to the considerably higher power consumption of audio recording and the battery capacity limits on current bio-loggers, it is unlikely that continuously logging raw audio would be a suitable sensor modality for long-term logger deployments. However, scheduling (e.g., sampling for only a few hours a day) could dramatically increase lifetime whilst still providing a sufficiently representative training set. Despite this drawback, we still demonstrated good model predictive performance using the audio labels and accelerometer features only. Thus, a small subset of animals can be equipped with audio and motion loggers to provide ground-truth calibration for a larger set of animals equipped only with motion loggers.

While we have primarily highlighted the use of audio for training behaviour classifiers, bio-loggers fitted with microphones may also be useful tools for other study purposes such as investigating how species respond to environmental acoustic stimuli or exploring patterns of animal vocal behaviour (Stowell et al., 2017; Wisniewska et al., 2018). The audio recordings collected from our bio-loggers often revealed the presence of other species (e.g., antelope and baboon alarm calls) and in some cases also allowed for the identification of captured prey species from the prey distress vocalisations. Such contextual information could be particularly useful where opportunities for visual observations are rare. Furthermore, we were able to identify more than 300 roar events from the 5 male lions in this study. This data alone could be used to assess vocalisation rates as well as provide insight into the spatial patterns of vocalisations when combined with GPS collar data.

In future, acoustic bio-loggers could be greatly enhanced by intelligent on-board processing functions aimed at reducing battery load by either limiting recording to sounds of interest or by storing audio variables rather than raw audio samples. Consideration must also be given to the mode of data retrieval with wireless data transmission being a preferred option. These advancements would be particularly beneficial to studies on smaller species, where battery capacity is limited, and elusive species, where logger retrieval is difficult.

Few published studies have reported the use of micro-sensors to investigate aspects of lion behaviour (Wilson et al., 2018) however, with advances in technology and the development of interdisciplinary research partnerships, opportunities to overcome previous study limitations have arisen. Gao et al. (2013) suggested that one of the main challenges associated with analysing accelerometer data from wild animals is that there is often very little observational data to generate an accurate behaviour classifier. We have demonstrated how on-animal audio recordings can be used to collect a large amount of ground truth data for training accurate classifiers. Acoustic bio-loggers have wide-ranging application and this work can inform the design and development of future bio-loggers for other animal behaviour studies.

DATA AVAILABILITY

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

SC-J, AL, and DM conceptualised the addition of audio sensors to bio-loggers. AM designed the bio-loggers and assisted in the extraction and analysis of data. Study animals were captured and fitted with bio-loggers by PT and BdP. MW carried out the data analysis and wrote the manuscript with input from all authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00171/full#supplementary-material

Audio 1 | Eating.

Audio 2 | Drinking.

Audio 3 | Fast.

Audio 4 | Slow.

Audio 5 | Stationary.

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Lions at the Gates: Trans-disciplinary Design of an Early Warning System to Improve Human-Lion Coexistence

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Across Africa, lions (*Panthera leo*) are heavily persecuted in anthropogenic landscapes. Trans-disciplinary research and virtual boundaries (geofences) programmed into GPS-tracking transmitters offer new opportunities to improve coexistence. During a 24-month pilot study (2016–2018), we alerted communities about approaching lions, issuing 1,017 alerts to four villages and 19 cattle posts. Alerts reflected geofence breaches of nine lions (2,941 monitoring days) moving between Botswana's Okavango Delta and adjacent agro-pastoral communities. Daily alert system costs per lion were US$18.54, or $5,460.24 per GPS deployment ($n = 13$). Alert-responsive livestock owners mainly responded by night-kraaling of cattle (68.9%), significantly reducing their losses (by $124.61 annually), whereas losses of control group and non-responsive livestock owners remained high ($317.93 annually). Community satisfaction with alerts (91.8%) was higher than for compensation of losses (24.3%). Study lions spent 26.3% of time monitored in geofenced community areas, but accounted for 31.0% of conflict. Manual alert distribution proved challenging, static geofences did not appropriately reflect human safety or the environment's strong seasonality that influenced cattle predation risk, and tracking units with on-board alert functions often failed or under-recorded geofence breaches by 27.9%. These insufficiencies prompted the design of a versatile and autonomous lion alert platform with automated, dynamic geofencing. We co-designed this prototype platform with community input, thereby incorporating user feedback. We outline a flexible approach that recognizes conflict complexity and user community heterogeneity. Here, we describe the evolution of an innovative Information and Communication Technologies-based (ICT) alert system that enables instant data processing and community participation through interactive interfaces on different devices. We highlight the importance of a trans-disciplinary co-design and development process focussing on community engagement while synthesizing expertise from ethnography, ecology, and socio-informatics. We discuss the bio-geographic, social, and technological variables that influence alert system efficacy and outline opportunities for wider application in promoting coexistence and conservation.

Keywords: *Panthera leo*, conflict mitigation, geofencing, socio-informatics, alert system, early warning, coexistence, grounded design

INTRODUCTION

Globally, large predators struggle with the consequences of human population growth and development. An iconic example is the African lion (*Panthera leo*). Lion numbers and distribution have decreased precipitously over the past century with many regional populations continuing to decline, putting them at risk of local extinction (Riggio et al., 2013; Henschel et al., 2014; Bauer et al., 2015). The situation is exacerbated along protected area boundaries where human retaliation for livestock losses and indiscriminate persecution can inflict heavy losses that reverberate throughout protected areas (e.g., Loveridge et al., 2016). Edge effects have far-reaching demographic consequences for lions (Woodroffe and Frank, 2005) and conflict with people remains the single biggest threat to their persistence. Particularly worrying is the continent-wide use of poison to control lions (Ogada, 2014; **Supplementary Data 1**) as this indiscriminate method also drives the declines of other endangered biota (Ogada et al., 2016).

Despite decades of applied conflict management research (Trinkel and Angelici, 2016; van Eeden et al., 2018), sustainable coexistence of rural communities with lions has yet to be achieved in many countries (Bauer et al., 2015). The successful mitigation of conflict primarily depends on changes in people's behaviors and risk management (Reddy et al., 2017), requiring trans-disciplinary research and conservation approaches that appropriately reflect the human dimensions of coexistence (Bennett et al., 2017; Pooley et al., 2017). This, inevitably, entails the direct involvement of rural communities in the design and testing of coexistence strategies. Because they bear the risks and costs of coexistence, Africa's communities are the key stakeholder of lion conservation outside protected areas. Mirroring a global omission in biodiversity conservation (Sterling et al., 2017), Africa's communities rarely have direct access to lion monitoring information and are often marginalized during conservation development processes.

Recent advances in Global Positioning System (GPS) tracking technology have revolutionized our understanding of wildlife movements and ecology (Kays et al., 2015). Beyond the mere tracking of fauna, innovative integrations of geofences (i.e., virtual boundaries that can trigger alerts when transgressed), automated data processing, and modern communication networks offer opportunities for use of wildlife tracking technology in various conservation contexts (Wall et al., 2014). For example, geofence applications can be designed to reduce human-induced wildlife mortalities (e.g., Sheppard et al., 2015). Dynamic geofencing can improve human safety by integrating near real-time processing of situational awareness, i.e., the continuous evaluation of relative risk (Zimbelman et al., 2017). In the case of lions and people (and their livestock), conflict typically manifests along well-defined land use and land tenure boundaries such as protected area edges. Simplistically, we can express conflict (the risk of undesirable interactions) as the probability of direct contact between these actors at any point in time. In other words, what is the real-time proximity of lions to people and livestock? Using proximity-based risk rules that are linked to geofences may, therefore, provide an opportunity to reduce the likelihood of conflict between people, their livestock, and lions. Informing people about the presence of lions in anthropogenic landscapes (by geofence triggered early warning) might enable them to exercise the changes in behavior upon which successful coexistence relies (Reddy et al., 2017).

The Okavango Delta lion population in northern Botswana represents one of the last strongholds for the long-term survival of the species (Riggio et al., 2013; Bauer et al., 2015). The Delta's eastern panhandle region constitutes a critical lion conservation area with on-going conflict (Weise et al., 2018), widespread persecution (**Supplementary Figure 1**) and important dispersal linkages with other lion areas in the Kavango Zambezi Transfrontier Conservation Area (KAZA-TFCA). In this anthropogenic landscape with multiple edges, we tested the efficacy of alerting rural communities about approaching lions to improve human and livestock safety. Here, we reflect critically on experiences from the system's 2-year pilot stage (**Figure 1**) with daily online data checks, static risk geofences, subjective evaluation of geofence breaches and manual alert distribution. We evaluate pilot study results in terms of conflict, technology performance, community satisfaction and feedback, financial costs, and the ecological implications for human and livestock safety. We provide details of the bio-geographic, social, and technological variables that influence alert efficacy. Following identification of the core challenges of effective early warning, we employed an adaptive, trans-disciplinary research design (**Figure 1**) to develop a versatile, autonomous, Information and Communication Technologies-based (ICT) lion alert system, capable of delivering near real-time alerts through interactive community interfaces. The evolution of this prototype platform was founded on a co-development strategy with maximum community participation and feedback. Our results highlight the importance of multi-disciplinary research that synthesizes ethnography, ecology, and socio-informatics. Finally, we outline opportunities for the platform's wider application in wildlife conservation.

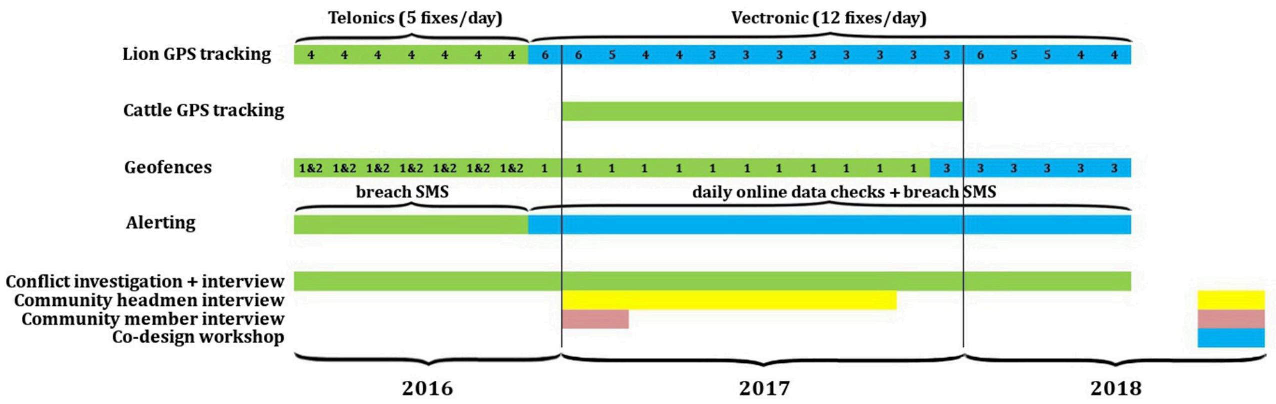

FIGURE 1 | Timeline of key research activities and lion alert system elements during the pilot study. Numbers in row "Lion GPS tracking" represent monthly sample sizes. Numbers in row "Geofences" indicate which virtual boundaries (see **Figure 2**) triggered alerts.

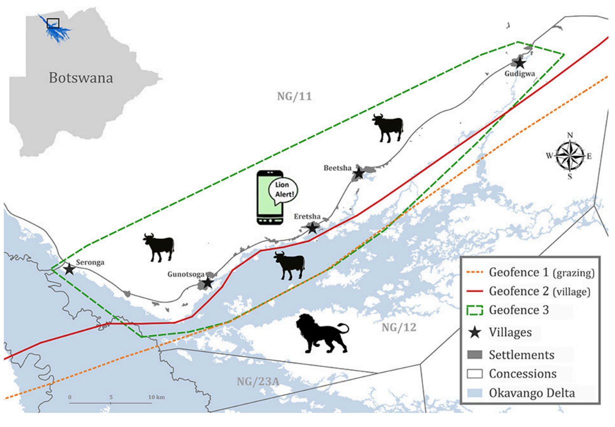

FIGURE 2 | Design of the lion alert system during the pilot study (May 2016–May 2018) showing the placement of virtual geofences across the study area in the northern Okavango Delta, Botswana. Geofences 1 and 2 were programmed into lion GPS tracking units deployed until end of 2017, Geofence 3 into units deployed from January 2018 onward.

MATERIALS AND METHODS

Study Area

Between 13 May 2016 and 12 May 2018 (the pilot study), we studied lions, conflict and cattle (*Bos taurus*) (**Figure 1**) across communities living at the boundary of the NG/11 and NG/12 multi-use areas (settlement, agriculture, livestock, and wildlife tourism) located along the northern edge of Botswana's Okavango Delta (**Figure 2**). The area supports high levels of biodiversity (Ramberg et al., 2006), forms part of UNESCO's 1000th World Heritage Site, Ramsar Site No. 879, and provides critical linkage habitat with protected areas in the KAZA-TFCA. The study area comprised five main villages, 44 remote cattle posts (i.e., small, often seasonal, homesteads with a cattle night enclosure), and intermittent settlements (**Figure 2**) with ~5,000 resident inhabitants from three ethnic groups, namely the Hambukushu, the Bayeyi, and the Basarwa (Mendelsohn and el Obeid, 2004). The main subsistence activities entail household-specific combinations of agro-pastoralism with small business; most families subsist on <$US 500 (hereafter $) monthly income. Increasing conflict with lions and elephants (*Loxodonta africana*) significantly impacts agro-pastoral households (Songhurst, 2017; Weise et al., 2018). Livestock are mainly a socio-cultural commodity; most cattle roam freely across unrestricted communal pastures shared with wildlife, and their management is haphazard, with minimal day-time herding (<10%) and irregular night-time confinement (~40%) in predator-proof enclosures (see Weise et al., 2018 for additional detail). Through herd counts, we estimated a total standing herd of 16,500 cattle in 2017. The Department of Wildlife and National Parks (DWNP) compensates livestock owners for lion-related stock losses at average national cattle market values (Department of Wildlife National Parks, 2013). Owners report livestock losses to the nearest DWNP or police office and compensation is granted following case-specific evaluation of the supporting evidence (for additional procedural detail see Songhurst, 2017).

The Okavango Delta experiences annually variable seasonal flooding (Murray-Hudson, 2009), the extent of which strongly influences the socio-ecology of lions (Kotze et al., 2018). We considered three climatic seasons: (1) Wet season (January–April) with rising flood levels, >80% of annual rainfall, and surface water availability in seasonal pans in NG/11; (2) Early dry season (May–August) with a progression from peak Delta flooding to low flood levels in NG/12, no rains, cold winter temperatures, and the drying up of seasonal pans in NG/11; and (3) Late dry season (September–December) with dry seasonal pans, consistently high mid-day temperatures (>35°C), minimal rainfall, and surface water restricted to the last permanent channels in NG/12. Detailed bio-geographic and socio-cultural descriptions are available from Mendelsohn and el Obeid (2004), Pröpper et al. (2015), and Sianga and Fynn (2017). The regional mix of dry savannah woodlands with wetland habitats provides critical functional heterogeneity of seasonal habitats for wild and domestic herbivores (Fynn et al., 2015; Weise et al., 2019).

Lion Tracking and Movement Analyses

We tracked nine adult study lions (four females, five males) from different social groups with combined VHF radio-GPS Iridium satellite transponders that enabled near real-time transmission of positional data and that were equipped with on-board geofencing functions. Tagging of specific lions focused on individuals with known or suspected conflict histories and was conducted in the immediate vicinity of communal grazing pastures. All GPS units were programmed to transmit geofence breach and exit SMS messages to the researchers. Transponders weighed <1.5% of adult body weight and were equipped with automated drop-off mechanisms. Until December 2016, we tracked four lions with Telonics TGW-4570-3 units (Telonics Inc., Mesa, AZ, USA) that recorded and relayed five daily locations, however switching into 2-hourly sampling mode when breaching Geofences 1 or 2 (**Figure 2**). From December 2016 onwards, we followed lions using Vectronic Vertex Plus v2.1 units (Vectronic Aerospace GmbH, Berlin, Germany) that transmitted GPS locations every 2 hours (h) (**Figure 1**). The six units deployed in December 2016 were programmed to report Geofence 1 breaches. Following the revision of geofences (see **Geofence Placement**), the three units deployed in January 2018 were programmed to report Geofence 3 breaches (**Figures 1**, **2**). At any one time, we tracked between three and six social groups simultaneously. In addition, we recorded lion group compositions and identification details (using whisker spot differentiation) during direct field monitoring and from high-resolution photographs that were sourced from wildlife tourism enterprises operating in the study area.

Because spatial outliers often represented lions entering community areas, we calculated seasonal home ranges as 100% Minimum Convex Polygons (MCP) (Mohr, 1947). We computed range metrics with QGIS 2.18 (QGIS Development Team, 2016) using the AniMove 1.4.2 (Boccacci et al., 2014) extension. We calculated home range centroids and percentage overlap with community areas using QGIS geoprocessing tools. For each lion, we also calculated the duration (minutes) between consecutive GPS locations. For any duration <250 min (nominally 4 h), we calculated the distance between locations using the Haversine formula (Sinnott, 1984), which compensates for the curvature of the earth's surface, and calculated the mean speed for that interval by dividing distance by duration. Speeds were converted to km/h for analysis purposes. Each speed calculation was assigned to a time of day using the midpoint of the associated time interval.

Cattle Tracking

Between January and December 2017, we deployed SPOT Trace^{TM} GPS tracking units on 42 domestic cattle (forty one females, one male) from 29 herds (see Weise et al., 2019 for additional herd and tracker details). Monitored cattle represented herds from four main villages and 18 cattle posts. Herds were sampled using a stratified-random approach that acknowledged each sampling location's proportional contribution to the study area's entire standing herd in 2017. At each location, specific herds were randomly selected from all local herds. Monitoring focused on lead animals and had no influence on the herd's management. We programmed trackers to record and relay GPS positions at hourly intervals, or, if trackers had been stationary for >1 h, at first detection of movement via an in-built motion sensor.

Geofence Placement

Prior to the pilot study's start in May 2016, we manually created static alert boundaries Geofences 1 and 2 (**Figure 2**) in Google Earth. Geofence 1 (grazing) reflected the known extent of livestock grazing areas (2015–2016), whilst Geofence 2 (village) represented the known subsistence activity area, i.e., the area where humans might encounter lions on foot. Geofence 1 had the primary objective of improving livestock safety by allowing owners to collect cattle from grazing lands as lion approached, whilst Geofence 2 aimed at improving human safety.

Based on a cumulative MCP that contained all human settlements and cattle posts, 95% of cattle GPS data recorded in 2017, and 90% of lion-related livestock depredation locations (pilot study cases), we created Geofence 3 as a static alert polygon in December 2017 (**Figure 2**). We discarded the outermost 5% of cattle positions and 10% of predation incidents as these reflected outliers of unguarded herds moving beyond community areas into tourism concessions. Geofence 3 served as an updated alert boundary and was programmed into lion GPS units deployed in January 2018 (**Figure 1**) with the objective of improving both human and livestock safety.

Alert Distribution

During the alert pilot study (13 May 2016 – 12 May 2018), we received geofence breach alerts from lion GPS units via SMS notification. Regardless of the time of day, we immediately relayed breach information to the headmen of all villages and cattle posts within 8.0 km linear distance of Geofence 1 (grazing land) breach locations, and within 5.0 km linear distance of Geofence 2 (village) breach locations. We informed all communities within 8.0 km linear distance of Geofence 3 breach locations, assuming that this window would provide a safety buffer of at least 2 h, sufficiently long to take precautions.

In agreement with traditional customs, we initially alerted village and cattle post headmen who had previously agreed to forward alerts to livestock owners in their communities. Each recipient then distributed messages further, resulting in a snowball distribution system. In the course of the pilot study, we expanded alert distribution to other community members who requested to receive alerts directly, e.g., conflict-affected livestock owners (see Conflict Investigations and Lion Conflict Involvement). Participation was voluntary and there was no discrimination by ethnicity, gender, age, location, or profession. We did not distribute accurate lion GPS latitude/longitude information but informed recipients about the identity of approaching lions and an approximated distance and direction. Geographically distinct villages and cattle posts were alerted separately.

Following alert malfunctions by the collars and the deployment of new transponders in December 2016, we also checked lion GPS locations online (via the manufacturer's data portal) at least twice per day (usually around sunrise and sunset) and alerted communities about geofence breaches in case collars did not detect breaches or failed to transmit breach SMSs (**Figure 1**). On randomly selected dates, we recorded the work effort for manual data checks and alert distribution. Additionally, we recorded all financial costs pertaining to the implementation of this pilot alert system, including any expenses for GPS units and data fees, veterinary fees, deployment expeditions, and staff cost for alerting effort.

Evaluation of Static Geofences

To evaluate the validity of initial geofences (Geofences 1 and 2; **Figure 2**), we calculated seasonal cattle-lion encounter risk levels as well as a human safety buffer calibrated by lion movement speed.

Seasonal Cattle-Lion Encounter Risk

We mapped all investigated lion-related livestock depredation incidents and seasonal cattle-lion encounter risk levels into a 1.0 km × 1.0 km grid of the study area. For each lion GPS location recorded in 2017 ($n = 13{,}503$), we determined the closest GPS time match for simultaneously tracked cattle ($n = 69{,}793$ locations), considering a maximum time difference of 6 h. We then calculated the separation distance between these locations using the Haversine formula (Sinnott, 1984). Based on distances, we assigned a preliminary risk level to all 1.0 km^2 grid cells that contained lion locations:

0 - No risk (separation >5.0 km);
1 - Lowest risk (separation <5.0 km and >1.0 km); and
2 - Intermediate risk (separation <1.0 km).

For all data points, we then determined the frequency of any cell being assigned as intermediate risk, and for multiple counts, refined the risk level by adding further levels as:

3 - High risk (lion-cattle separation distance <1.0 km occurred 2 or 3 times); and
4 - Vertically high risk (lion-cattle separation distance <1.0 km occurred >3 times).

Any cells containing investigated lion kills were assigned level 4, very high risk.

Human Safety

To calculate the human risk area, we created a 5.5 km radius circular buffer around each human settlement. The value for this radius is based on the maximum hourly distance traveled by any lion in this study. We then mapped buffers into a 1.0 km^2 grid of the study area, and marked each cell whose centroid overlapped within any of the buffer zones. The ensemble of marked cells comprises the human risk area.

Conflict Investigations and Lion Conflict Involvement

Livestock owners voluntarily reported depredation incidents by carnivores for further investigation. During investigations, we recorded attack location (latitude/longitude), date, time, livestock characteristics and value, evidence of responsible carnivore species and their numbers, details of protective measures and herd management, and the owner's opinions about conflict lion management, compensation of losses, and the lion alert system. To allow for a guided process with maximum flexibility, we employed semi-structured interviews (Brockington and Sullivan, 2003) that were administered through open and closed questions. All respondents participated voluntarily and anonymously. We also recorded all livestock loss claims to large carnivores reported to the local DWNP office. These data have no accurate GPS reference and are collated at the village level.

To determine the involvement of study lions in investigated depredation incidents, we cross-referenced each incident location against all lion GPS data 24 h before and after the event. We used a proximity-association rule to infer responsibility. We considered study lions as responsible for an incident if: (1) they were directly observed at the site; (2) they were located within 250 m of the attack site within 6 h of the estimated attack time; or, in case positional data were sparse, (3) they were located within 500 m of the attack site within 12 h of the estimated attack time.

Community Perceptions and Feedback

For a grounded understanding of human-lion interactions, researchers need to grasp the complexity of social circumstances that influence community life, interactions with predators and conflict (Dickman, 2010; Pooley et al., 2017). During this study, we maintained a permanent research presence in the northern Okavango Delta. We conducted several semi-structured interview surveys (**Figure 1**) that yielded important insights into the various dimensions of conflict and social practices of the alert system's stakeholders.

In addition to interviews with conflict-affected livestock owners ($n = 78$; see section Conflict Investigations and Lion Conflict Involvement), we recorded conflict lion management suggestions from a randomly sampled control group of livestock owners ($n = 53$). Again, we asked their opinions about conflict lion management, the government's compensation scheme, and the lion alert system. For 12 months preceding the pilot study, and during alert distribution, we recorded livestock depredation by lions in terms of number of livestock lost, percentage stock loss, and financial value. Furthermore, we interviewed all senior village headmen ($n = 12$) using open-ended questions. Regardless of current wildlife legislation and conflict mitigation activities tested by the researchers, we asked headmen to state their three main aspirations about how conflict lions should be managed. For all interviews, we grouped common answers and ranked them in order of priority, assigning weight scores of 3, 2, and 1 in declining order.

To determine community perceptions of the pilot alert system across the wider community, we also conducted a qualitative study using a participatory action research approach (Kemmis and McTaggart, 2005) (**Figure 1**). Social scientists interviewed a randomly sampled group of local inhabitants, trying to understand how local residents perceive and deal with lions, given the presence of a pilot system designed to improve the terms of coexistence. Semi-structured interviews ($n = 36$) were conducted in those villages with highest conflict. For triangulation of responses, we included a diverse group of people that comprised different ages, both genders, varying levels of education, and from different villages and cattle posts (**Supplementary Data 2**). A local assistant translated questions into one of the three main local languages (Setswana, Hambukushu, Bayeyi). Interviews focused on the daily life of participants, the use of digital technologies and their integration into routines, knowledge, and attitudes toward lions, the lion alert pilot system, and the participant's social life in the community. Researchers documented visits via field notes, video, and photos, transcribing insights on the day of interviews. All interview materials were analyzed using qualitative content analysis (QCA) (Schreier, 2014). Analyses focused on key aspects relating to the conflict mitigation potential of the pilot lion alert system. Analyses were corroborated by external researchers who had not been involved in interviews. We took care to use findings from different researchers and interview series to ensure a broad perspective and to offset any observer bias.

Community Co-design Workshops

Following the pilot study, we involved communities in the design of an autonomous ICT-based lion alert platform (**Figure 1**), intended to distribute alerts flexibly and automatically, and to a larger group of recipients. Similar to social media, the transformed alert system has a user interface, thus requiring direct community feedback during the development phase for effective implementation. The study communities are diverse in terms of their ethnicity, languages, socio-economic status, cultural traditions, literacy (Mendelsohn and el Obeid, 2004; Hanemann, 2005; Songhurst, 2017), and exposure to modern communications technology (Ertl, 2018). Consequently, a variety of technological, cultural and individual barriers could inhibit the efficacy of an ICT-based lion alert distribution platform (Irani et al., 2010; Mutula et al., 2010; Vitos et al., 2017; Ertl, 2018).

We conducted co-design workshops in Gunotsoga, Eretsha, and Beetsha, the villages that had experienced highest conflict and received most alerts (**Figure 3**). To facilitate maximum community consultation, workshops followed a participatory design approach (Schuler and Namioka, 1993). We developed prototype designs for different telecommunication devices and purposes using the Axure (2017) tool. Printed and digital illustrations were used to visualize the existing system (**Supplementary Figure 2**) as well as proposed outputs under an autonomous platform (**Supplementary Figures 3, 4**). Paper versions were utilized to engage target groups with limited experience in technology use (Gubbiotti et al., 1997; Vitos et al., 2017). Workshop participants ($n = 35$) comprised traditional village leadership, Village Development Committee chairpersons, representatives of local farmers' associations, livestock owners, and herdsmen, with an age range from 21 to 80 years. These represented a large degree of diversity in terms of occupation, location, age, literacy, herd sizes (range: 1–220), husbandry practices, conflict with lions, and experience with the pilot alert system (**Supplementary Data 3**). Workshops lasted between 2.5 and 4 h and participants were divided into two working groups per village.

In each village, co-designing involved a two-tiered process with a pre-defined set of workshop implementation guidelines. Initial workshops focused on assessing and discussing experiences, benefits, and challenges from the lion alert pilot study while also reflecting on system elements and processes (**Supplementary Figure 2**). These workshops included focus group interviews (Byrne and Sahay, 2007; Pruneau et al., 2018), mapping and creative ideation and discussion sessions (Gubbiotti et al., 1997; Pruneau et al., 2018), in which participants expressed their aspirations and expectations toward alert delivery by an autonomous platform. Following several days of reflection, follow-up workshops focused on iterating the existing system and co-designing the functionality of the autonomous platform, capturing specific user requirements. Participants tested our preliminary, printed or digital designs (**Supplementary Figures 3, 4**), which we modified according to their feedback.

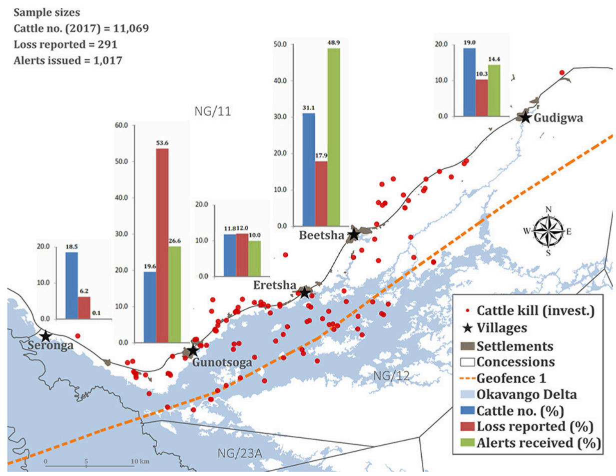

FIGURE 3 | Proportional distribution of cattle, livestock losses to lions, lion alert messages received and investigated (invest.) conflict locations across the study area in northern Botswana. Except for cattle holdings that were determined in 2017, data represent the lion alert pilot study from 13 May 2016 until 12 May 2018.

During this step-wise consultation process, we discussed all elements pertaining to the data acquisition phase, data processing, system components, and future alert output and distribution. We determined literacy levels, the types of communication technology used, and their integration into daily routines. Further, we determined user-specific preferences regarding alert frequencies, alert contents, message formats (i.e., text, image, sound, or voice message) in relation to telecommunication devices, and languages. Combining users' needs and new functions, we designed a feedback portal that allows for independent user registration and reporting of lion encounters in community areas, livestock movements and depredation events.

RESULTS

All means are presented ± one standard error.

Conflict Summary (2015–2018)

Prior to alerting (May 2015–April 2016), depredation by lions affected 63.7% of livestock owners, with a mean annual loss of

TABLE 1 | Reported livestock losses to carnivores with associated compensation value ($US), 13 May 2016–12 May 2018.

Species	No. of incidents	Percentage	Cattle	Goats	Horses	Donkeys	No. of livestock	Percentage	Compensation value in $US	Percentage
Lion	255	87.9	282	0	3	6	291	87.1	80,814.00	97.8
Wild Dog	26	9.0	30	0	0	0	30	9.0	1,591.00	1.9
Leopard	8	2.8	5	4	0	0	9	2.7	226.00	0.3
Caracal	1	0.3	0	4	0	0	4	1.2	0.00	0.0
Total	290	100	317	8	3	6	334	100	82,631.00	100

Source: Department of Wildlife and National Parks, Seronga office.

4.1 ± 0.7% of stock owned (range: 0–60.0%; $n = 102$). This is equivalent to a mean of 1.8 ± 0.2 livestock per owner (range: 0–13) and a mean compensation value of $319.12 ± $408.67 per owner (range: $0–$2,351.00).

During the pilot study (13 May 2016–12 May 2018), community members directly encountered lions on at least 57 occasions (i.e., those reported to the researchers), including one near-fatal incident in which a male lion attacked a group of livestock owners (seriously injuring one person) who had attempted to kill the animal. In addition, livestock owners reported 290 incidents of livestock depredation by carnivores to the DWNP, with an annual compensation value of $41,316 (**Table 1**). Lions were responsible for >87% of reported predation incidents and total livestock lost (**Table 1**). Due to different compensation valuation rules (Department of Wildlife National Parks, 2013), lion-related losses amounted to >97% of the total compensation value (**Table 1**). Lions predominantly predated on cattle (96.9% of livestock killed) (**Table 1**). The associated impact was not evenly distributed across the study area; Gunotsoga village incurred disproportionately high losses in relation to cattle numbers (**Figure 3**). Depredation was highest during low-flood months (September–February), comprising 60.8% of incidents ($n = 255$) and 61.5% of stock losses ($n = 291$) (**Supplementary Data 4**). At this time, lions have unrestricted access to communal grazing pastures and cattle roam further into core lion habitat by following receding flood waters in NG/12, thereby increasing depredation risk significantly (Weise et al., 2019).

Lion Movements and Geofence Transgressions

Seasonal Home Range Overlap With Community Areas

Corresponding with the Delta's flooding regime, lion home range sizes and percentage overlap with geofenced community areas were highly variable, exhibiting strong seasonality (**Figure 4**; **Supplementary Figure 5**). Males had significantly larger seasonal home ranges than females ($U = 20$; $Z = -2.76$; $p = 0.006$), whereas females, on average, spent nearly twice as much time in geofenced community areas (**Table 2**). This was influenced by females PleoF003 and PleoF005 raising cubs in community areas. Seasonal home ranges were largest during the late dry season (**Figure 4**) when lion movements are no longer restricted by seasonal flooding. Home range overlap with community areas was highest during the wet season (**Figure 4**) when wild lion prey like plains zebra (*Equus burchelli*) and Cape buffalo (*Syncerus caffer*) follow early rains and migrate out of the Delta into NG/11 dryland grazing areas causing a northward shift in lion home ranges (panels c and f in **Supplementary Figure 5**). Seasonal home range overlap with geofenced community areas significantly decreased ($r_{ho} = -0.756$; $p < 0.001$, $n = 25$) with increasing home range centroid distance to the nearest settlement (**Supplementary Figure 6**).

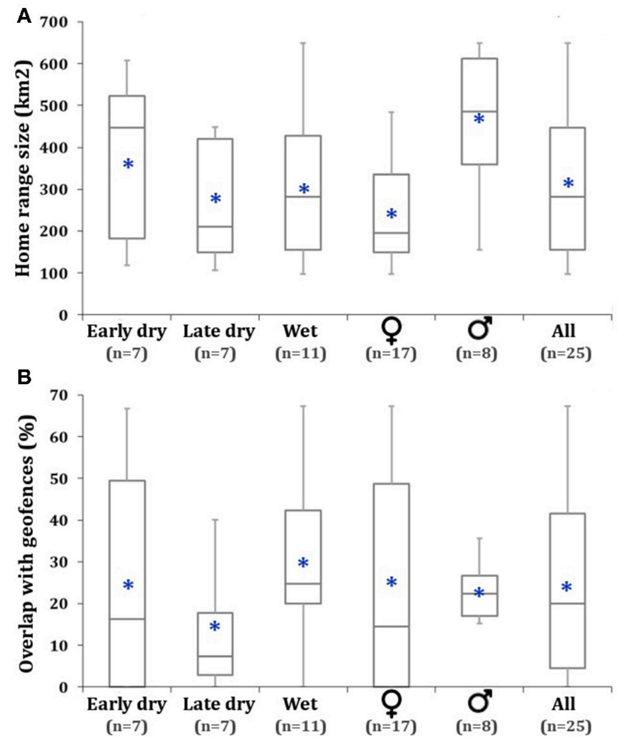

FIGURE 4 | Comparison of 100% Minimum Convex Polygon lion home range size **(A)** and percentage home range overlap with geofenced community areas **(B)** by season and genders. Blue asterisks show mean values. Sample sizes are shown in parentheses. The early dry season lasted from May to August, the late dry season from September to December, and the wet season from January to April. 100% MCPs were only calculated for individuals with sufficient GPS data (>60 days).

Lion Activity

Study lions were predominantly nocturnal, exhibiting peaks in movements between 16.00 and 05.00 local time (**Figure 5**).

TABLE 2 | Summary of lion monitoring, geofence breaches, and alerts issued during the pilot study.

Lion ID	GPS days	Alerts issued (incl. reminders)	Geofence breaches	Mean duration ±SE (hours)	Minimum (hours)	Median (hours)	Maximum (hours)	GPS hours	Percentage inside geofence	Percentage outside geofence
PleoF001	730	0	1	2.0 ± 0.0	2.0	2.0	2.0	17,520	0	100.0
PleoF003	730	367	37	205.2 ± 105.4	2.0	22.0	3,866.0	17,520	43.3	56.7
PleoF004	118	0	5	10.4 ± 4.3	2.0	8.0	26.0	2,826	2.0	98.0
PleoF005	511	239	51	146.4 ± 57.5	2.0	32.0	2,150.0	12,264	60.9	39.1
Females subtotal	2,089	606	94	160.8 ± 51.8	2.0	27.0	3,866.0	50,130	30.2	69.8
PleoM001	73	0	2	9.0 ± 1.0	8.0	9.0	10.0	1,726	1.0	99.0
PleoM005	290	33	25	38.9 ± 11.2	2.0	8.0	188.0	6,946	14.0	86.0
PleoM006	380	275	22	54.0 ± 13.9	2.0	26.0	248.0	9,120	13.0	87.0
PleoM009	98	74	19	66.1 ± 44.3	6.0	26.0	862.0	2,354	53.4	46.6
PleoM010	24	10	4	14.0 ± 4.7	8.0	10.0	28.0	578	09.7	90.3
Males subtotal	865	392	72	48.5 ± 12.9	2.0	18.0	862.0	20,724	16.8	83.2
All individuals ($n = 9$)	2,954	998	166	112.1 ± 30.1	2.0	24.0	3,866.0	70,854	26.3	73.7
Un-collared individuals		19	–	–	–	–	–	–	–	–
Total	2,954	1,017	166	112.1 ± 30.1	2.0	24.0	3,866.0	70,854	26.3	73.7

*See **Supplementary Data 8 and 9** for additional lion tracking details.*

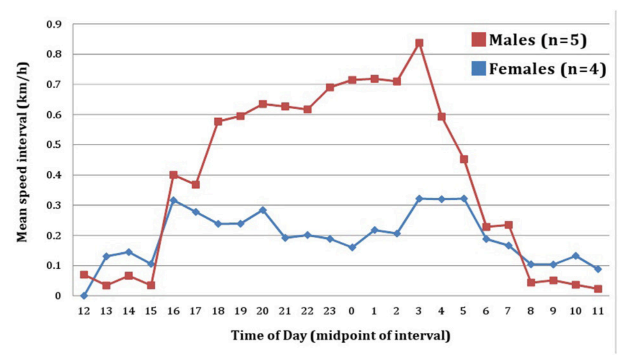

FIGURE 5 | Mean movement speed of lions by hour of day. Speed was inferred by measuring displacement between successive GPS fixes, adjusted to hourly intervals.

Correspondingly, 81.4% of lion attacks on livestock with known time of day ($n = 97$) occurred during night hours, significantly more than during the day ($\chi^2 = 38.36$; df = 1; $p < 0.001$). While males and females exhibited similar activity rhythms (**Figure 5**), males, on average, moved 2.63 ± 0.26 times faster during peak activity hours, and with a maximum speed of 5.47 km/h.

Geofence Transgressions

Study lions spent 26.3% of all time monitored within geofenced areas (**Table 2**), with a mean of 21.9 ± 8.0% per individual (range: 0–60.9%; $n = 9$). Geofence transgressions were highly variable in terms of frequency and duration (**Table 2**). Four of the nine study lions only sporadically breached geofences (cumulative $n = 12$) (**Supplementary Figure 5**), whereas five lions accounted for 92.8% of all breaches (**Table 2**), and with a bias toward females ($\chi^2 = 2.91$; df = 1; $p = 0.088$), two of which raised seven cubs to >12 months age in community areas. During cub-rearing, individual transgressions by females lasted as long as 89.6 days and 161.1 days, respectively, whereas the median duration of transgressions across all individuals was 24 h (**Table 2**). Due to cub-rearing, female transgressions, on average, lasted significantly longer than those of males ($T = 1.86$; $p = 0.032$).

Lion Conflict Involvement

We investigated 116 (45.5%) of the 255 lion-related livestock predation incidents reported for compensation (**Table 1**) and cross-referenced depredation sites against GPS paths. Spatial association analyses showed that the nine study lions were responsible for 36 incidents (31.0%), whilst un-tagged lions accounted for the majority of investigated losses (69.0%). This result demonstrates the effect of partial sampling (i.e., low population representation by tagged study lions) on alert utility. From a total of 277 lion observations (88 by researchers, 189 from tourism sources with photo evidence), we estimated that the nine study lions represented 12.3% of all resident individuals (>24 months age) and 41.2% of known female prides and male coalitions in the study area.

All study lions that transgressed geofence boundaries were involved in livestock depredation, but males were significantly more conflict prone when controlling for monitoring time ($\chi^2 = 4.98$; df = 1; $p = 0.026$). The two females that reared cubs in community areas were involved in 58.3% ($n = 21$) of all depredation incidents involving study lions. The four

TABLE 3 | Community conflict lion management suggestions during the pilot study.

Statement content	All respondents $n = 90$		Community headmen $n = 12$		Livestock owners affected by lion conflict $n = 78$	
	Frequency	**Weight score**	**Frequency**	**Weight score**	**Frequency**	**Weight score**
1. Remove lions from community livestock lands by translocation, fencing or lethal control.	70	192	5	13	65	179
2. Improve livestock husbandry and protection (herding, kraaling etc.).	23	42	2	3	21	39
3. Increase/improve government compensation for livestock losses.	17	38	3	7	14	31
4. Collar more lions for alert distribution.	16	36	1	3	15	33
5. Provide alternative cattle water sources and/or move livestock away from the Delta.	12	24	5	11	7	13
6. No active management of conflict lions.	8	19	3	6	5	13
7. Other (e.g., deterrence).	9	17	3	6	6	11
8. Collect more information for community education.	6	11	3	6	3	5
9. No comment.	6	–	2	–	4	–
Total	167	377	27	56	140	321
MANAGEMENT CHARACTERISTICS OF RESPONSES						
Physical separation of people/livestock from lions	82	206	10	24	72	182
Reactive/symptomatic strategy	87	230	8	20	79	210
Proactive/protective strategy	60	116	11	23	49	93
Laissez faire/no-interference strategy	14	30	6	12	8	18

Answers represent community expectations recorded between October 2016 and May 2018 and were weighted, assigning scores of 3, 2 and 1 in declining order of priority. If individual livestock owners were interviewed multiple times, the most recent answers were considered for analyses.

individuals with home range centroids nearer settlements (<10.0 km distance) and highest home range overlap with community areas (>33.3%) were significantly more involved in conflict ($\chi^2 = 25.31$; df = 1; $p < 0.001$), accounting for 86.1% ($n = 31$) of incidents attributable to study lions.

Manual Alert Distribution

Alerts Issued (May 2016–May 2018)

We alerted the community about approaching lions on 188 days, or 25.8% of study days, representing 366 lion alert days when considering multiple animals on the same day. In total, we sent 1,017 alert SMS to 66 recipients in four villages and 19 cattle posts (**Table 2**; **Supplementary Data 5**). Alert messages represented 166 geofence breaches (males: 72; females: 94) resulting in 304 original alerts and 694 reminder messages when lions spent prolonged periods in community areas, as well as nine incidents of un-tagged lions detected near cattle posts (19 alerts) (**Table 2**). Five lions accounted for 97.1% of alerts issued (**Table 2**), with females disproportionately represented ($\chi^2 = 45.88$; df = 1; $p < 0.001$). Reflecting the variable movements of individual study lions (see Lion Movements and Geofence Transgressions) and the contribution of un-collared individuals to depredation (69.0%), the distribution and frequency of alerts (**Figure 3**; **Supplementary Data 6**) differed significantly from that expected by livestock losses (χ^2 = infinite value; df = 4; $p < 0.001$).

Effort

The mean daily researcher effort for retrieving and checking location data of 3–6 active collars and associated alert distribution via SMS messages on 116 randomly selected days was 40.8 ± 1.1 min (range: 14–71 min). The number of active units weakly correlated with daily effort ($r_{ho} = 0.142$).

Community Opinions, Aspirations, and Actions

Livestock and Conflict Lion Management

QCA of 36 semi-structured interviews revealed that people value their livestock for reasons other than monetary income. Livestock are predominantly a cultural commodity, provide food security (especially in times of drought when crops fail), and are sold context-dependently, e.g., when owners pay school fees or funeral costs. Respondents regarded livestock husbandry as a full-time commitment, yet very few employ herders (Weise et al., 2018). Based on the narratives of daily life routines, husbandry entails night-time kraaling, release of herds in the morning hours, and searches for stray animals.

Interviews with 12 community headmen and 78 depredation-affected livestock owners yielded 161 conflict lion management suggestions that reflected eight common themes. The majority of responses entailed removing lions from community land by lethal control, translocation or effective fencing, comprising 50.9% of the total priority weight (**Table 3**). This mirrors results from QCA such that the majority perception of lions was negative (75.0%, $n = 27$). Together with improvements of general livestock protection and the state-funded compensation scheme, expansion of the lion alert system featured among secondary lion management approaches, ranking fourth in terms of overall priority weight (**Table 3**). The alert system's priority weight was higher for conflict-affected livestock owners (10.3%) than community headmen (5.4%). In terms of conflict management characteristics, most community members expected a form of physical separation from free-ranging lions (54.6% priority weight), corresponding with QCA results in that community members felt that "*coexistence with lions was not possible.*" Lion management suggestions were significantly biased toward symptomatic, reactive mitigation strategies (61.0% priority weight), followed by proactive, protective strategies (30.8% priority weight) and no-interference management approaches (8.0% priority weight) (**Table 3**) ($\chi^2 = 121.76$; df = 2; $p < 0.001$).

Community Satisfaction With Lion Alerts and Compensation

Livestock owner satisfaction was higher for alerts than the state-funded damage compensation scheme. Of all 78 livestock owners interviewed during depredation investigations, 65 commented about their perceptions of the alert system and compensation scheme. Of these, 56.9% had previously received compensation for losses, whilst 75.4% had previously received lion alerts (**Supplementary Data 7**). Only 24.3% of compensation recipients ($n = 9$) were satisfied with the compensation scheme. QCA showed that compensation did not improve people's situation. Instead, respondents felt "*left alone*" as the DWNP does not have the resources to attend to their lion conflict reports. The key reasons for dissatisfaction included "*insufficient compensation amounts*" (85.7%, $n = 24$) and/or "*delayed compensation payments*" (35.7%, $n = 10$).

Conversely, 91.8% of lion alert recipients found messages beneficial ($n = 45$), whilst 6.1% ($n = 3$) stated that they "*no longer wished to receive them.*" QCA corroborated that, despite prevailing uncertainties about appropriate responses to approaching lions, the pilot alert system was perceived as beneficial and respondents requested its "*continuation and expansion.*" Of the 65 conflict-affected livestock owners, 90.8% ($n = 59$) wished to receive lion alerts via SMS in the future (**Supplementary Data 7**).

Actions Following Alerts

The 45 livestock owners who perceived alerts as beneficial stated different benefits and actions. The most common response was livestock kraaling for increased night-time protection (68.9%), followed by changes in cattle grazing directions and areas (15.6%), setting of deterrence fires at homesteads (4.4%) and active herding of cattle (2.2%). Other stated benefits included a feeling of increased personal security due to awareness about lion presence (13.3%) and an improved understanding of lion movements and ecology (17.8%). However, another 32 alert recipients stated that they did not take actions because they "*did not know what to do*" (59.4%) and/or "*feared dangerous encounters with elephant, buffalo or lions during night hours*" (81.3%). QCA confirmed that community members "*rarely encounter lions,*" contributing to an uncertainty of how to respond when direct interactions occur.

Conflict Mitigation Potential

During the pilot study, mean annual livestock losses of those owners who acted upon alerts ($n = 49$) significantly decreased in terms of number of stock lost ($U = 876.5$; $Z = -2.29$; $p = 0.021$), compensation value ($T = -2.38$; $p = 0.021$) and percentage of stock lost ($T = -3.07$, $p = 0.003$) (**Figure 6**). Their mean annual losses were significantly less than those incurred by a randomly sampled control group ($n = 53$) in terms of number of stock lost ($U = 945.5$; $Z = 2.36$; $p = 0.018$), compensation value ($T = -2.34$; $p = 0.010$) and percentage stock loss ($T = 1.91$; $p = 0.029$) (**Figure 6**), despite 23 control group livestock owners (43.4%) also regularly receiving lion alerts but choosing not to act. By comparison, prior to receiving alerts (2015–2016), mean annual losses did not differ significantly between alert-sensitive livestock owners and control group owners (number of livestock lost: $U = 1209$; $Z = 0.596$; $p = 0.548$, compensation value: $T = 0.14$; $p = 0.440$, percentage stock lost: $T = 1.424$; $p = 0.078$) (**Figure 6**). There were no significant changes in the mean annual number of stock lost ($U = 1308$; $Z = -0.60$; $p = 0.541$), mean compensation value ($T = 0.48$; $p = 0.628$) or mean percentage stock lost ($T = 0.88$; $p = 0.379$) when comparing pre-alert and pilot study losses incurred by control group livestock owners (**Figure 6**). Alert-sensitive livestock owners reduced losses even though reported lion depredation increased by nearly 300% during the pilot study: year 1 = 74 livestock, year 2 = 214 livestock. In financial terms, livestock owners who acted upon alerts reduced their mean annual loss to lions by $124.61 (59.6%), equivalent of a percentage stock loss reduction of 3.4% (**Figure 6**). During the pilot study, the mean annual loss incurred by alert-sensitive livestock owners was $134.40 less (57.7%) than that by control group livestock owners (**Figure 6**).

Financial Cost and GPS Collar Performance

Financial Cost

Considering all associated expenses, the total cost of GPS-collaring nine adult lions for inclusion in the alert system was $70,983.04 ($n = 13$ deployments), with a mean deployment cost of $5,460.24 ± $493.89 for units equipped with on-board geofence breach technology (range: $3,821.10–$10,764.40). GPS tracking technology and associated data fees contributed 46.8% to the total cost, whilst veterinary expenses accounted for 44.5% of the total, the remainder accruing from local staff, vehicle, and expedition expenses. The 13 geofence-enabled units were active for a total of 3,829 tracking days [including days for first units prior to commencement of the pilot study ($n = 888$)], giving an approximate daily alert system cost of $18.54 per lion. Daily cost would decrease to $4.99 if all units had operated until the end of their expected lifetimes.

In light of an annual livestock damage of approximately $40,407 caused by lions (**Table 1**), and assuming that early warning would effectively prevent depredation, the observed daily alerting cost merits the inclusion of only six lions (8.2% of

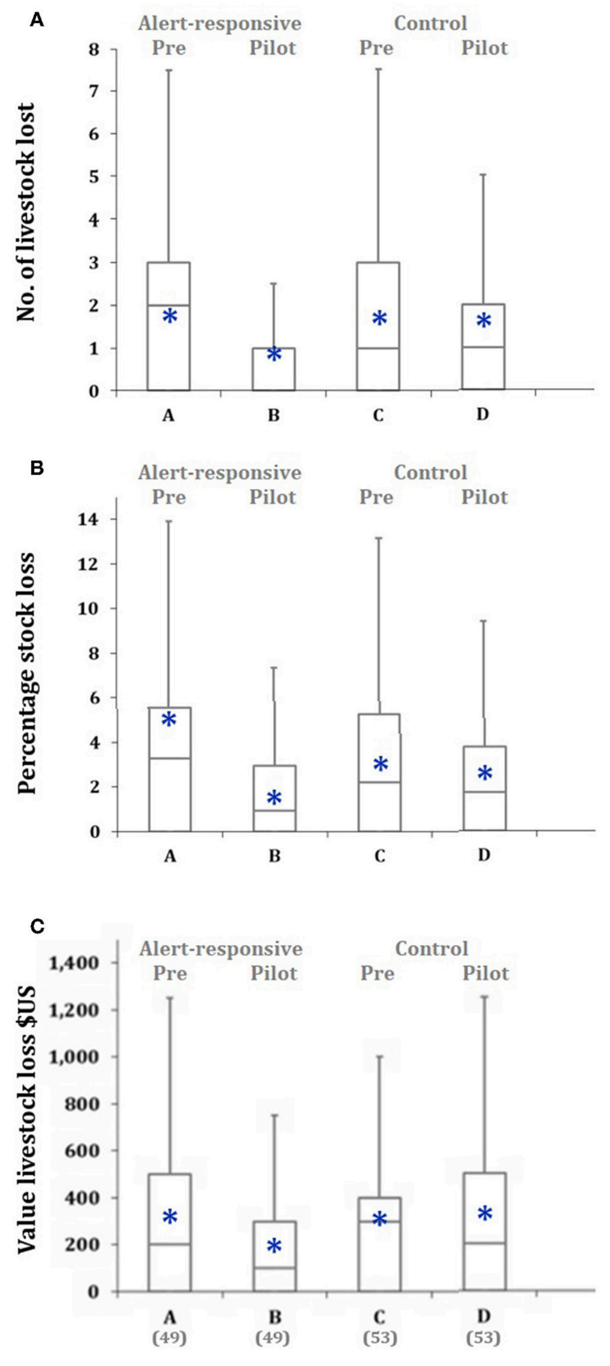

FIGURE 6 | Comparison of annual lion-related livestock losses **(A)**, percentage stock loss **(B)**, and associated compensation value ($US) **(C)** for responsive alert recipients before (A) and during alerts (B) and a control group of non-responsive recipients before alerts (C) and during alerts (D). Blue asterisks show mean values. Sample sizes are shown in parentheses. Livestock losses were recorded from May 2015 until April 2016 for the pre-alert phase and from November 2016 until October 2017 for the alert phase.

the estimated population), whereas 22 individuals (30.4% of the population) could be included if GPS units functioned reliably. Early warning financially breaks even if the inclusion of a specific lion, on average, can prevent the depredation of 12 livestock per year, emphasizing that GPS tracking efforts need to be focused on habitual livestock raiders.

Collar Performance

Lion GPS data

The performance and reliability of GPS tracking units was highly variable in terms of complete daily tracking data received (range: 2.3–92.6%; **Supplementary Data 8**) and the proportion of scheduled GPS locations received (range: 51.1–95.9%; **Supplementary Data 9**). We replaced four active collars in December 2016. At the end of the pilot study, four units still transmitted data daily, whereas three units (23.1% of deployments) malfunctioned between 22 and 71 days after deployment, and two units were deactivated following lion deaths.

During the pilot study, GPS units ($n = 13$ deployments) delivered complete data sets on only 28.8% of all lion tracking days ($n = 2{,}941$ with a 24 h cycle), with a mean of 27.9 ± 7.7% per deployment (**Supplementary Data 8**). Increasing the GPS sampling frequency from five daily locations (Telonics units, $n = 875$ tracking days) to 12 (Vectronic units, $n = 2{,}066$ tracking days) decreased the daily success rate of receiving complete data from 55.9 to 17.3%, respectively. There was no significant difference in the mean percentage of complete GPS tracking days between collars fitted on male ($n = 7$ deployments) and female ($n = 6$ deployments) lions ($U = 10$; $Z = -1.50$; $p = 0.133$). Despite the low number of complete tracking days, the 13 transmitters delivered 83.3% of the expected 29,609 lion GPS locations (**Table 4**; **Supplementary Data 9**). The mean percentage of scheduled GPS fixes received per lion was 81.2 ± 1.6% (range: 74.8–87.3%, $n = 9$). A randomized sample of 286 GPS data gaps (both collar types combined) showed that GPS fix and transmission failures resulted in a mean data gap duration of 6.9 ± 0.3 h (range: 0–124 h). The modal duration of GPS data gaps was 4 h, with maximum durations of 36 h for Telonics units (five daily locations) and 124 h for Vectronic units (12 daily locations).

Detecting geofence breaches and alert issuing

Early GPS units (May–December 2016) were programmed to report both geofence breaches and exit events. These transponders detected 44 geofence breaches, including 42 Geofence 1 transgressions and two Geofence 2 transgressions. However, in 22.7% of cases ($n = 10$), breach messages were only received after lions had already left the geofence again, in 15.9% of cases ($n = 7$) the units failed to transmit exit messages, and in 11.4% of cases ($n = 5$) the units failed to transmit breach messages but reported exits. Compared with lion movement paths plotted from GPS locations, on-board geofence functions under-detected true Geofence 1 breaches ($n = 51$) by 17.6%, whilst missing 80.0% of true Geofence 2 breaches ($n = 10$) across 6 months of operation. In combination with delayed breach messages, the community received alerts about 74.5% of true Geofence 1 breaches ($n = 38$) and 30.0% of true Geofence 2 breaches ($n = 3$), the latter including one reminder. These irregularities caused us to return to daily manual data checks and alert distribution.

TABLE 4 | Proportions of expected and received GPS fixes from geofence-enabled lion tracking collars.

Gender	Unit 1 (expected)	Unit 1 (received)	Percentage	Unit 2 (expected)	Unit 2 (received)	Percentage	Total (expected)	Total (received)	Percentage
Female	2,204	2,111	95.8	19,781	16,427	83.0	**21,985**	**18,538**	**84.3**
Male	2,672	1,663	62.2	4,952	4,455	90.0	**7,624**	**6,118**	**80.3**
All units (*n*=13)	4,876	3,774	77.4	24,733	20,882	84.4	**29,609**	**24,656**	**83.3**

*See **Supplementary Data 9** for details of individual lions and deployments.*

Moreover, of the nine units deployed subsequently (December 2016 and January 2018), four (44.4%) did not detect any geofence breaches (although they occurred), whilst three (33.3%) failed altogether within 11 weeks of deployment.

Seasonal Cattle Depredation Risk and Human Safety

Based on a GPS distance matrix of lion and cattle GPS locations, and the locations of investigated lion conflict, **Figure 7** shows the seasonal distribution of lion risk to cattle. Very high risk was widespread during the early wet season when lions still had unobstructed access to communal grazing lands before annual floods arrive, and two females raised cubs in community lands. Arbitrarily defined Geofence 1 (i.e., the original grazing lands boundary) contained 88.2 and 91.3% of high and very high risk cells during the wet and early dry seasons, respectively. However, as the risk interface progressively changed throughout the year, moving in relation to receding flood waters, Geofence 1 only contained 59.5% of high and very high risk cells during the late dry season, revealing the need for dynamic geofencing that appropriately reflects seasonally changing environmental conditions and associated predation risk.

Similarly, **Figure 8** demonstrates that the arbitrarily drawn village safety boundary (Geofence 2) only partially protected human settlements. Geofence 2 contained only 75.4% of the estimated 1,278 km^2 risk area and excluded one cattle post while another was partially excluded. Additionally, 24 cattle posts and two villages appeared too close to Geofence 2 to permit sufficient time for adequate precaution. Based on a 1 h human safety buffer calibrated to the maximum hourly speed recorded for any lion (5.47 km/h), safety alerts should be triggered further from village areas and cattle posts. Human settlements change over time, requiring dynamic geofencing to reflect these changes (e.g., adjusted Geofence 3, **Figure 2**).

Community Co-design Workshops

The communities are technologically marginalized, with sporadic access to electricity and the Internet. Despite these infrastructural challenges, mobile phones are ubiquitous in this rural part of Botswana (as elsewhere in Africa) and are, therefore, an ideal medium for receiving alerts. All workshop participants ($n = 35$) owned mobile phones but predominantly used these for basic functions such as calling relatives. The prevalence of feature and smart phones varied by village (**Figure 9**), with an overall smart phone representation of 23.5%. Participant literacy was low (62.9%), digital literacy even lower (14.3%), compromising the delivery of lion alerts via text or image messages only. Community members speak five different languages, with Setswana being the only one common to everyone. For future alerting, desired message formats differed geographically and a combination of image and voice messages was most popular (**Figure 9**). Respondents remarked that feature phones prohibit the use of imagery to convey all necessary alert information (lion distance and direction), necessitating combinations with text and voice formats (**Supplementary Figure 3**). Participants also suggested the incorporation of specific sounds and ringtones (e.g., lion roar) to distinguish alerts from other messages.

Workshop participants advocated for the development of an information feedback loop in the form of a community portal with application interfaces that enable users to report their own lion observations and depredation incidents, but also to retrieve lion alert information independently. Respondents commented that such a portal would improve reporting speed and ease while relinquishing the reliance on private mobile devices, which may not be charged or have insufficient credit for reporting. Co-design workshops also revealed the need for additional digital literacy training and community mapping of the local environment to enable accurate reporting of feedback via digital maps (Mapedza et al., 2003; Vitos et al., 2017). The preferred method of ensuring personal data security and privacy was password protection, which participants knew from social media. Meanwhile, 30 min was the preferred frequency of lion information updates on the portal. The variety of user-specific requirements and contexts demonstrates the necessity for a flexible, customized lion alert platform that provides a range of interactive features.

Autonomous System Design With Automated Alerts

In combination with the logistical and technological challenges encountered during the pilot study, community co-design workshops prompted the development of an autonomous, automated lion alert platform (**Figure 10**). This development provides maximum versatility in terms of data acquisition and integration, geofence creation, alert distribution, and community participation. The system's key features and capabilities are outlined in **Box 1** and **Supplementary Figure 4**.

The new system is based on the computation of implicit surfaces for defining dynamic geofences. It automatically retrieves, and integrates, positional data from any actors equipped with GPS transponders as well as supporting environmental information from online databases (e.g., seasonal

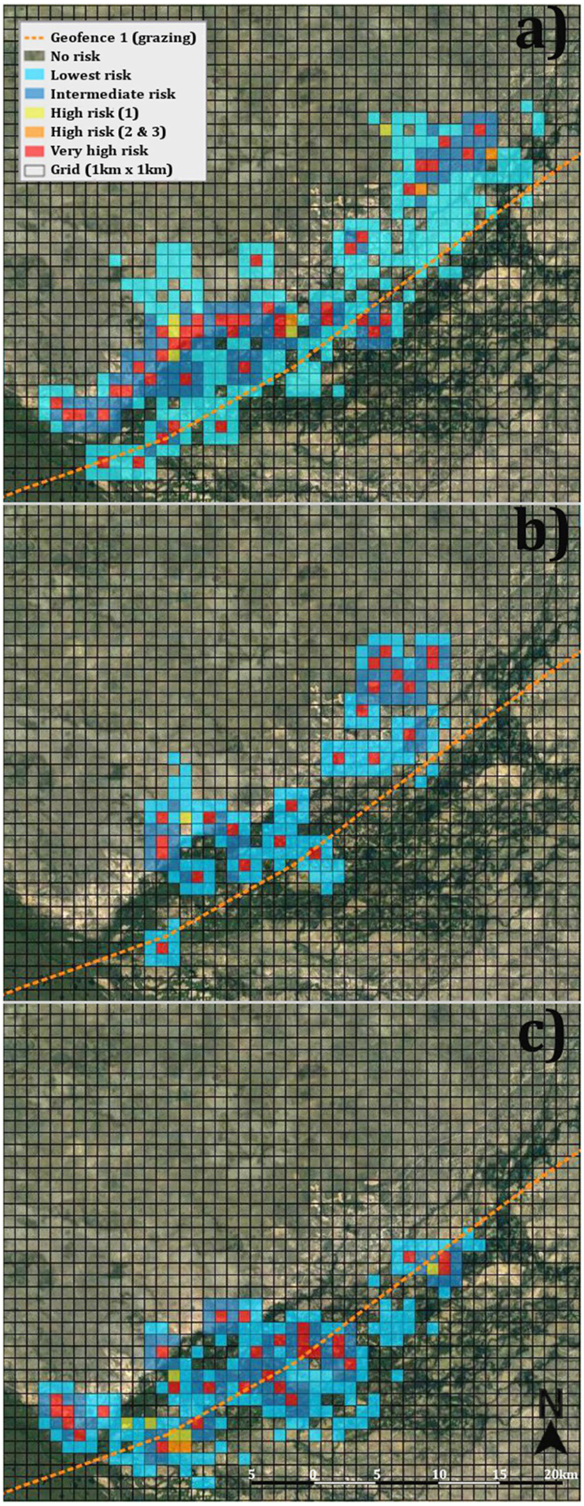

FIGURE 7 | Seasonal geo-assessment of lion risk to cattle, showing **(a)** the wet, **(b)** the early dry, and **(c)** the late dry seasons of 2017. Risk levels are mapped into a 1.0 km × 1.0 km grid across the study area. Each grid cell is hot-cold color-coded to indicate relative risk level. Yellow (1) and orange (2 or 3) indicate the number of instances in which lions approached to within 1.0 km of tracked cattle. Red cells are those in which either kills occurred, or there were >3 records of lions within 1.0 km of tracked cattle.

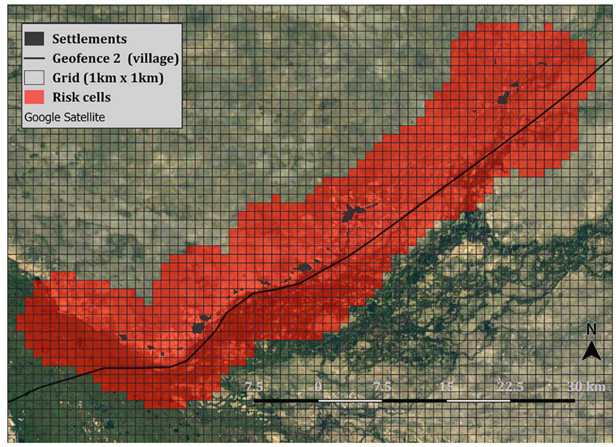

FIGURE 8 | Comparison of Geofence 2 placement with geo-assessment of lion risk to people. Risk was calibrated to the maximum hourly speed moved by any lion in this study (5.47 km/h) and mapped into a 1.0 km × 1.0 km grid across the study area. Red cells indicate risky areas within 1 h distance from permanent settlements.

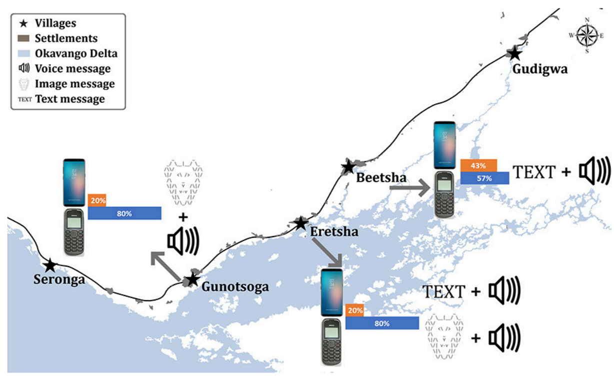

FIGURE 9 | Village-specific use of feature and smart phones and expected lion alert message formats as determined during co-design workshops.

flooding levels). Virtual boundaries can be adjusted either manually or by machine-learning algorithms that process GPS and other relevant data in near real-time, predicting risk areas while automatically adjusting geofences. Conflict is defined by empirically determined risk thresholds (e.g., see Seasonal Cattle Depredation Risk and Human Safety). Based on our results, the literature, and community feedback, we identified 26 key variables (**Supplementary Data 10**) that influence conflict likelihood and, therefore, require empirical consideration in computation of flexible geofences. We developed the prototype in Java with Java Database Connectivity for a Structured Query Language. The system is currently implemented on a Windows 2016 server with PostgreSQL. Depending on the type of tracking technology utilized, it can be compartmentalized into GPS storage with data processing on any other platform. Autonomous data integration and processing removes reliance on predefined, static geofences and on-board alert functionality. The system is

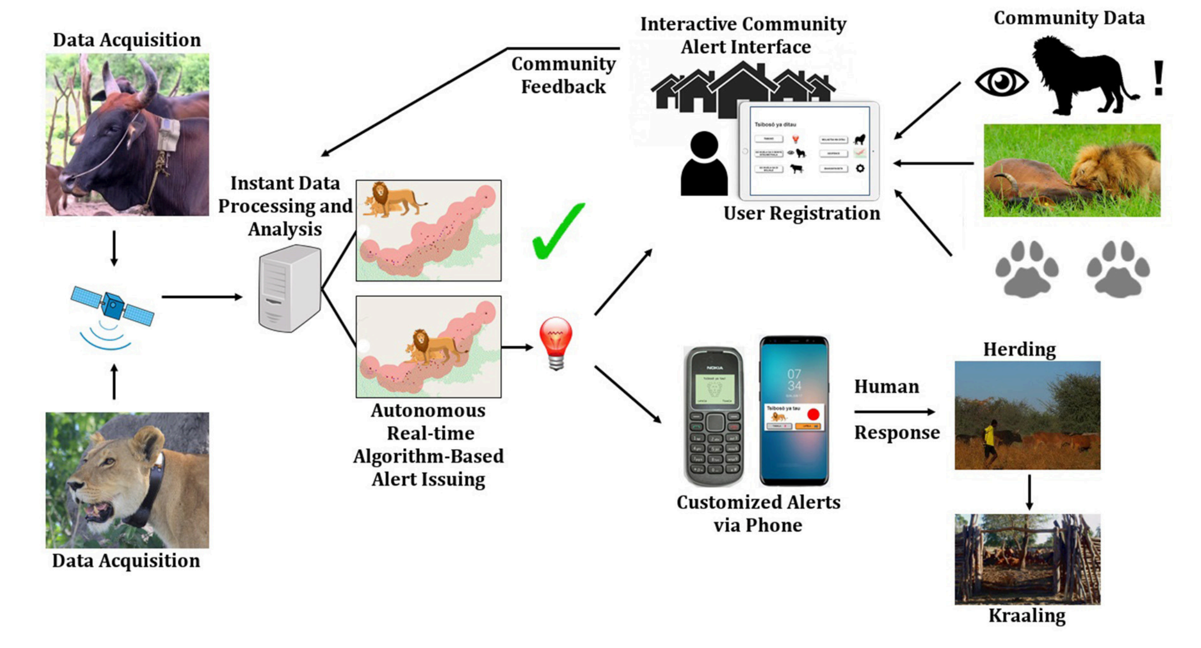

FIGURE 10 | Visualization of the autonomous, automated lion alert system with key features and functionalities.

Box 1 | Key features and capabilities of the autonomous lion alert system.

1. Real-time integration of diverse environmental data and community feedback (e.g., lion encounters, cattle movements, depredation sites);
2. Autonomous, objective geofence computation based on available input data and a priori threshold setting (e.g., critical distances and areas);
3. Flexible implementation of village-specific geofences;
4. Dynamic geofencing, including static and mobile virtual boundaries, and possible attractors and deterrents for depredation;
5. Automated, instant alert delivery via multiple media formats to a diversity of communication technology devices;
6. Integration and configuration of risk evaluation parameters;
7. Interactive community portal with data report and entry interfaces;
8. Independent user registration;
9. User-specific selection of preferred alert message types (text, image, sound, or combinations thereof) and languages based on literacy levels and communications technology; and
10. Options for alert delivery via social media platforms (e.g., WhatsApp or Facebook groups) or supporting devices such as sirens and light installations.

currently hosted at the Department of Economic Disciplines, Faculty III of Siegen University, Germany.

The platform enables independent, password-secured and anonymous user registration via cell phone number (**Supplementary Figure 4A**). Subscribers can then select their preferred alert format for different phone types (e.g., **Supplementary Figure 3**). We designed alert applications for smart and feature phones, ensuring that feature phones provide the same functionalities. Registered users receive alerts instantly. Instead of data processing time, alert frequency is determined by the sampling regime of GPS transponders and the availability of corroborating data.

To enable maximum community participation and ownership as well as system sustainability, we co-designed a suite of alert portal interfaces (**Supplementary Figure 4**). These will be accessible via tablet computers installed at each village's administrate office, with guidance provided by specially trained community members. Interfaces include an overview of current and past alerts, the reporting of lion encounters or tracks, the reporting of depredation incidents, information on lions, display of geofence(s), and personal settings (**Supplementary Figure 4**). All features are delivered in Setswana language. Following others (Medhi et al., 2006; Vitos et al., 2017), we utilized visual elements to support interface use by illiterate subscribers. Map interfaces are currently based on distance zones that resemble active geofences, an approximation that was understood by workshop participants. In future, digital maps will provide an intuitive avenue for reporting of relevant information according to geo-physical landmarks such as trees, lagoons, and islands that all community members can relate to. For feature phones, we programmed USSD-based (locally used to recharge phone credit) and voice-prompted reporting interfaces that have shown success in other participatory design projects (Weld et al., 2018). For illiterate users, automated voice prompts will be used to replace text prompts. Similar speech-based interfaces have successfully been tested with illiterate target groups (Raza et al., 2018). The autonomous platform allows for the instant integration of community feedback into alert calculations (**Figure 10**), increasing the representation of un-tagged lions in alerting and community ownership of the process.

DISCUSSION

Managing undesirable human-wildlife interactions requires adaptive strategies. In northern Botswana, communities seek safety from lions, primarily via physical separation and lion control. However, the continued lethal removal of damage-causing lions threatens population viability (Loveridge et al., 2016; Trinkel et al., 2017); fencing is expensive (Packer et al., 2013), ecologically problematic (Trinkel and Angelici, 2016), and can shift problems elsewhere (Osipova et al., 2018); while translocations are resource-intensive and have historically shown low success rates (Stander, 1990). By default, separation undermines coexistence. Consequently, separation also compromises the sustainable conservation of large free-ranging lion populations (Creel et al., 2013) that depend on connectivity between key ecosystems in human-inhabited conservation landscapes such as the KAZA-TFCA (Cushman et al., 2016). Early warning by geofence-triggered alerts provides an alternative mechanism that facilitates non-lethal and non-permanent separation at flexible spatio-temporal scales. Our study demonstrates that alerting rural livestock owners about approaching lions promotes improvements in livestock protection that result in significantly reduced losses, thereby facilitating the behavioral changes that coexistence requires (Reddy et al., 2017). Despite the immediate benefits of improving human and livestock safety, the success of early warning depends on effective system implementation by overcoming a variety of technological, human, and environmental challenges (**Box 2**).

The efficacy of lion alerts directly hinges upon user responses. To enable responses, the system needs to deliver messages to a variety of communication devices in a timely and understandable fashion (Medhi et al., 2006; Sherwani et al., 2009). Considering the user community's heterogeneity in terms of literacy, attitudes toward modernization, use of communication technology, and language and message style preferences, this poses challenges (**Box 2**). Careful pre-studies of the socio-cultural contexts, co-design of the system's functionalities, and alert distribution via modern socio-informatics are imperative to engage users satisfactorily and sustainably. For example, a user-friendly device for community data collection, the *CyberTracker*, provides adaptable, yet easily understandable, interfaces that are designed to enable geo-referencing of environmental information by rural inhabitants with different educational backgrounds (Ansell and Koenig, 2011). Co-design workshops revealed the need for information feedback loops that enable active participation in risk management, thus increasing community ownership. Instead of eroding traditional environmental skills and practices, an ICT-based alert platform provides an interactive avenue for their propagation and inclusion in environmental decision making (also see Ansell and Koenig, 2011). Other, maybe less apparent, benefits of a participatory strategy include the community's perception of "*being heard,*" improved digital literacy, and access to WiFi through the installation of community alert portals in remote villages.

Human-lion conflicts are complex (Dickman, 2010) and early warning efficacy strongly depends on our ability to quantify risk and its many drivers (**Supplementary Data 10**). In the Okavango Delta, lions and their wild and domestic prey live in a seasonally changing ecosystem (Murray-Hudson, 2009; Fynn et al., 2015). Changes in conflict likelihood correspond with seasonality as it influences lion and cattle movements, associated predation risk, and lion socio-ecology (Kotze et al., 2018; Weise et al., 2019). Translating these ecological changes, and their high levels of spatio-temporal variation, into risk probabilities in near real-time is a central prerequisite for alert efficacy, one that requires dynamic geofencing. It also requires intensive monitoring of different ecological variables (**Supplementary Data 10**) and can benefit from machine learning to infer behavioral patterns from animal GPS data (Valletta et al., 2017). Early warning will be most effective in situations where boundaries are clearly definable. Geofence design and breach detection must account for the speed of actors, likelihood of attack, and GPS fix schedules. With an ability to travel up to 5.47 km in 1 h, lions could breach geofences and enter villages without detection, even with short GPS fix intervals that considerably reduce transponder battery lifetime. Static geofences programmed into GPS transponders cannot sufficiently reflect the variability of ecosystems and conflict complexity. Here, we present an autonomous platform for the instant computation of dynamic geofences and flexible delivery to a variety of users.

Human-lion conflicts and their effective mitigation are scale-dependent (Montgomery et al., 2018a). The conservation benefit of individual- or group-based conflict mitigation methods decreases as economic cost increases in relation to population size (Shivik, 2004) and conflict area. Therefore, expensive interventions such as alerting are most feasible in conflict hotspots with highest conservation significance (e.g., by maintaining effective connectivity between populations), and where the majority of actors can be tracked cost-effectively. At the currently high cost of intensive GPS monitoring (Thomas et al., 2011), the on-going implementation of an early warning system requires significant resources, especially in high conflict zones bordering protected areas where lion mortality is high (Trinkel et al., 2017) requiring frequent tagging of new actors. We demonstrate the importance of appropriate population representation as our study lions accounted for 31% of the regional conflict. Partial collaring of the lion population resulted in focal alerting, not always benefiting the communities with highest losses. Alert systems will be most meaningful where the movements of actors and the effects of local attractors (e.g., cattle post locations or seasonally shifting prey density) can be combined into risk proxies that are computed as changing virtual boundaries. Tracking technology failures prevented the effective monitoring of lions and the detection of geofence breaches (**Box 2**), thus decreasing alert efficacy. Autonomous implementation of geofencing and alert functions through a stand-alone platform not only provides maximum system flexibility but also increases alert reliability. With continuous advances in modern animal tracking systems in terms of unit size and weight, cost, and independence from on-board battery supply (Tomkiewicz et al., 2010; Thomas et al., 2011), the feasibility of GPS-tagging actors increases, thus also improving the scalability of early warning and its overall cost-efficiency by reducing labor effort.

Box 2 | Opportunities and challenges of lion alerts identified during the pilot study.

Opportunities:

1) Increasing human safety by preventing dangerous encounters, e.g., during subsistence activities;
2) Encouraging livestock protection and husbandry practices (e.g., herding and kraaling);
3) Reducing livestock depredation, thus increasing food and economic security;
4) Improving tolerance of lions in human-dominated landscapes;
5) Increasing awareness and knowledge about local lions and their ecology; and
6) Advancing digital literacy and intra-community communication in partner communities.

Challenges:
Anthropogenic

1) Manual alert distribution depends on researcher/manager effort (and availability) in terms of checking GPS units daily and issuing alerts;
2) Risk of misuse of alert information to persecute lions;
3) Geofence breach messages dispatched by collars may be missed during night hours when breach probability is highest;
4) Alert distribution via community SMS snowball system is subject to intra-community relationships—not all farmers may receive messages from others;
5) System's effectiveness depends on human response to alerts;
6) Risk of increasing resentment toward and fear of lions via continuous reminders of their presence, i.e., artificial reinforcement of perceived threats;
7) Non-probabilistic, subjective interpretation of breach messages, and lion movement trajectory by researcher/manager is prone to human error, introducing the risk of informing the wrong communities;
8) Risk of desensitizing people to the relative threat posed by lions via frequent reminders of their presence without direct dangerous interactions;
9) Subjective selection of focal lions by researchers may bias population representation—conflict lions may exhibit strong avoidance of humans, thus being under-represented in the monitored sample;
10) System components may be difficult to understand for rural communities with little previous exposure to modern communications technology;

Technology

11) Efficient alert distribution via cell-phone network depends on reliable network coverage in remote areas, but also power supply to charge phones, retrieve GPS data, and distribute alerts—in January 2017, the system collapsed during the rainy season when public power supply and network coverage was insufficient during a high conflict period;
12) Limited reliability and accuracy of GPS-tracking technology causes delays in distributing alerts, influencing alert frequency, timing, and relevance;
13) On-board geofence functions are static and may not operate reliably or timely;
14) Lifespan of GPS-tracking technology limits system effectiveness and feasibility;

Ecology

15) Impact of tagging only one individual per group: lion mortality, changing group compositions and variable cohesiveness, immigration, and emigration affect population representation and system effectiveness;

Information

16) System effectiveness is scale-dependent—appropriate population representation (i.e., tagging all adult lions/groups simultaneously) across large areas is difficult to achieve in terms of financial feasibility and logistics; and
17) Objective, probabilistic establishment of relevant geofences requires a wealth of empirical bio-geographic data that may not always be available, or difficult to obtain (**Supplementary Data 10**).

We can use lions and livestock depredation as conflict proxies for a universal challenge, the increasing interface between people, livestock and wildlife. Globally, 262 wild terrestrial vertebrates, including 53 threatened species, interact detrimentally with people (Torres et al., 2018). Our lion alert platform is neither species- nor context-specific, lending itself to various conservation applications (also see Wall et al., 2014). Amongst others, possible scenarios include elephants approaching human settlements or crop fields (human and food security), a rhino leaving the safety of a reserve core management area (biodiversity security), or a buffalo herd approaching cattle (disease transmission risk). In each of these cases, the risk of an undesirable interaction is defined by critical distance thresholds, expressible as a likelihood of interaction and risk. As more and more wildlife are tracked via GPS (Kays et al., 2015), and advances in both animal-borne and non-invasive technologies provide cheaper and more reliable sensor options, the feasibility of implementing alert systems in human-dominated wildlife habitats increases. Our autonomous platform can be tailored to any risk scenario, given that the relevant vector data are available and conflict risk can be expressed in an algorithmic manner. In the case of alerting communities about lions, the new system permits the evolution from an experienced-based pilot phase into an experimental phase. Reducing human errors associated with manual alerting, for example by subjective interpretation of lion movement trajectories toward specific cattle posts or villages, is paramount.

An automated, autonomous platform provides a robust and objective mechanism with maximum versatility for creating dynamic, ecologically relevant virtual conflict boundaries and maximum flexibility in issuing customized alerts in a timely and culturally appropriate fashion. Successful conflict mitigation, via methods such as alerting, is highly context-specific and usually cannot be inferred from disciplinary knowledge alone. It requires adaptive co-design that encompasses local knowledge, a detailed understanding of the affected parties, and relevant research findings (Pooley et al., 2017; Montgomery et al., 2018b). Here, we chose a trans- and multi-disciplinary development approach involving local stakeholders as well as researchers from different disciplines to progress "from a science for society to a science with society" (Scholz and Stauffacher, 2009). The inherent complexity of human-carnivore conflict, both ecologically (**Supplementary Data 10**) and socio-culturally (Dickman, 2010), demands a direct and constructive collaboration between science and society. This interaction needs to identify and address the different dimensions of conflict and, therefore, can only be realized with a multi-disciplinary research and development strategy (Pooley et al., 2017; Montgomery et al., 2018b). Omission to do so will inevitably result in unsustainable or ineffective conflict mitigation efforts, particularly if the safety or livelihood of rural communities is at stake. System automation does not provide a panacea, however, as it cannot resolve all the challenges of early warning (**Box 2**). For instance, the utility of any early warning system, autonomous or otherwise, strongly depends on the rigorous identification and continuous tracking of its key actors. We demonstrate that this can be costly and difficult to achieve. Therefore, care should be taken to avoid reliance on early warning as a stand-alone mitigation method. The prototype alert platform (**Figure 10**), alongside other conflict reduction measures such as vigilant full-time herding (Weise et al., 2019), will be implemented in 2019, including further refinement of system processes and monitoring of its efficacy.

Alerting communities about lions devolves important ecological knowledge and sensitive information to Africa's key lion conservation stakeholders, the people that live with lions. It encourages active risk management, thereby moving beyond the symptomatic treatment of damage. Recipient communities, however, are not homogenous. In addition, technological limitations, the complexity of human-carnivore conflicts, and the variability of the natural environments in which these occur, complicate effective early warning, which requires a combination of expertise that synthesizes ethnography, ecology, livestock management, conservation psychology, and socio-informatics. Our development of a versatile, autonomous lion alert platform emphasizes the critical importance of a trans-disciplinary approach to mitigating human-lion conflicts.

ETHICS STATEMENT

We conducted research under permit numbers EWT 8/36/4 XXVII (61) and EWT 8/36/4 XXXVIII (63) granted by the Ministry of Environment, Wildlife and Tourism in Botswana. We interviewed human subjects and monitored livestock and lions with ethics approval from the University of Pretoria (no.: EC170525-120, EC170525-120a) and the Institutional Animal Care and Use Committee of the University of Massachusetts (Protocol no.: 2014-0083).

AUTHOR CONTRIBUTIONS

FW, AS, KS, HH, KA, MWH, MH, VW, and MT conceived the ideas and designed the methodology. FW, HH, KA, MT, and KS collected the data. FW, KS, HH, KA, and MH analyzed the data. FW, HH, AS, KS, MWH, and MS wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00242/full#supplementary-material

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Race and Gender Bias in the Research Community on African Lions

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We used bibliometric data to show that Black, African, and women researchers are underrepresented among authors of field studies on lions (*Panthera leo*) in Africa. This may lead to biased representation in institutions dealing with lion research and conservation and reinforce disenfranchisement with one of the most emblematic species in Africa. We discuss the causes, and ways for the lion research community to become more inclusive.

Keywords: ***Panthera leo*****, black, African, women, author, diversity, representation, inclusion**

INTRODUCTION

Race and gender issues have a profound impact on society. Race is sometimes considered fluid, outdated, and overtaken by social categories perceived to be more important like ethnicity and religion in shaping inequities and injustice (Kothari, 2006), but it remains an important determinant especially in the context of conservation (Garland, 2008; Kepe, 2009; Mbaria and Ogada, 2016). However, frank discussions about race are still rare and often controversial (White, 2002) and so is research that examines racial bias in science and its consequences for the content and use of science. Available literature focuses on the role of social injustice in conservation practice (Brockington and Wilkie, 2015; Kinzig and McShane, 2015; Mollett and Kepe, 2018), but there is also some literature on geographical representation among conservation science editors (Campos-Arceiz et al., 2017) and among conservation authors (Karlsson et al., 2007). Similarly, gender bias has been described in academic literature, and in Science, Technology, and Mathematics (STEM) in particular; women scientists on average publish, earn, participate in collaborations, and get funding less than their male counterparts but there is no clear consensus on the reasons (West et al., 2013; Wang and Degol, 2017; Grogan, 2018; Holman et al., 2018). Here we look in more detail at authorship of scientific papers on lions (*Panthera leo*) in Africa. We did not look at literature on Asiatic lions, since their study and conservation in India is practiced by a distinct and separate community.

Conservation research in Africa is often performed with (co-)funding from philanthropic or institutional development organizations, e.g., as part of integrated conservation and development projects. Among these organizations' aims is local capacity building and gender inclusiveness, which is often mentioned as one of the objectives of many such projects. Most African nations will also have relevant policy, and often research permits are contingent on inclusive participation in research projects. These factors potentially promote diversity among lion researchers, but power imbalances may lead to dominance of groups with more privileges and/or a stronger academic recognition. Others have found race to be a relevant factor in lion conservation in the field (Rust et al., 2016), here we analyzed race and gender bias in the composition of the lion research community. We place this work in the academic field of race studies where the use of Black to describe racial identity is conventional and omnipresent; in conservation literature this may be perceived as stigmatizing and politically incorrect.

METHODS

We aimed to work with a database of field studies on African lions, published in English academic journals. In July 2018, we downloaded citation data of papers with "*Panthera leo*" in the title, abstract, or keywords from seven databases going back to the year mentioned in brackets: Biological Abstracts (1949), PubMed (1974), Science Direct (1974), Scopus (1965), Web of Science (1995), Wildlife and Ecology Studies (1964), and Zoological Records (1969). We used EndNote to remove duplicates and included entries that contained the words "*Panthera leo*" in conjunction with "African lion" without further scrutiny. From the remaining list, we manually removed entries based on paleontological work or health and anatomical work based on captive lions, entries on lions in India, and entries that were included due to journals' species indexing (for example: mountain lion, sea lion, lion's share, Gulf of Lion). Finally, we read the abstracts of the remaining papers to exclude false positives. Our initial search criteria will have excluded lion papers that didn't use the species name in the title, abstract, or keywords (false negatives). Our EndNote database is available on request.

For all authors with three relevant papers or more, we categorized race, nationality, and gender of the individuals; the lion research community is strongly networked and collectively we knew over half personally, for others we used profiles from public internet sources such as social media, researchgate, and staff pages of university websites, or by contacting others who knew the person. We used only binary classifications; Black vs. non-Black, male vs. female, and nationality from an African vs. non-African nation. These classifications were based on phenotype; we actually found very little ambiguity and the classification process was fairly easy, if time-consuming. Classification of nationality for people we did not know personally, or by proxy, was based on publicly available elements of life history and may have been more ambiguous. We used the minimum of three papers as an arbitrary but logical threshold for two reasons: (a) it would be prohibitively resource intensive to do the categorizations for more than a few hundred authors and (b) we propose three papers as a reasonable threshold to distinguish a lion researcher from an author with a passing interest in lion research. We also listed affiliations and categorized them by whether the postal address was in or outside Africa, but since affiliations may change during an individual's career, analysis was more complex and limited to authors with six papers or more. This resulted in a classified list of authors publishing lion-based research up to July 2018.Since this is primarily a bibliometric study, combined with publicly available information, we did not seek ethical clearance for this research.

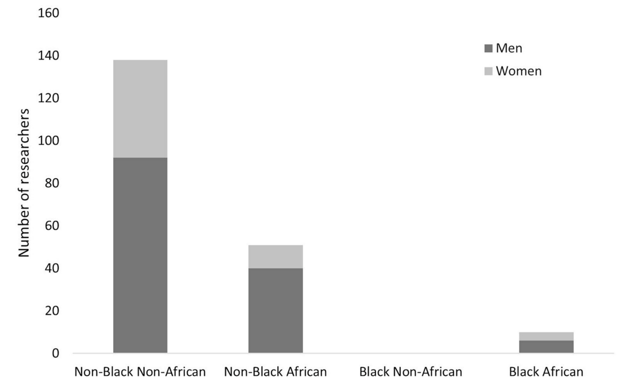

FIGURE 1 | Number of researchers with ≥3 papers on lions, by race, gender, and continent-aggregated nationality.

RESULTS

Our initial search found 1,752 unique entries; after cleaning we had a list of 615 papers of interest. We found that, out of 199 authors with ≥3 lion papers, only 10 were Black, 61 were Africans, and 61 were women (**Figure 1**). Among the Black Africans the nationalities represented were Benin, Cameroon, Kenya, Tanzania, and Zimbabwe; four were women. We found 50 non-Black researchers that were African nationals, but none who were Black with non-African nationality. Most non-Black African researchers were from South Africa, whereas we found no Black researchers from that country.

Diversity was not much different among the sub-set of 51 researchers with ≥6 papers (4 were Black and 18 were women). Affiliations in this group showed a slightly more positive pattern than nationality; 21 had an affiliation in Africa, of which 13 in South Africa. Most prominent on this list was the University of Oxford (nine affiliated researchers, including three in the top-six), followed by the universities of Minnesota, Leiden, Port Elisabeth and Pretoria, and the non-governmental organization Panthera (three or four each).

DISCUSSION

Our race, gender, nationality, and affiliation classifications were based on accessible sources; it was impractical to conduct an in-depth analysis of the ancestry of each researcher or to ask for self-classification. Actually, self-classification is not necessarily better since race is a social construct that reflects how one is seen by others (e.g., a self-identified non-Black perceived as Black will be treated as Black). However, with half of the classifications based on direct acquaintance and the other half based on a wealth of public information, we argue that the potential for misclassification was limited. Error in race and gender classifications is typically below 5% for face pictures only (review in Han et al., 2015; probably much lower when full body pictures and biographies were available), so misclassifications are unlikely to undermine our conclusions.

For listed researchers in Africa, we found no researchers of ostensible mixed race and the dichotomy Black/non-Black was unproblematic for a meaningful analysis of representation in the specific context of research on the African lion. Among listed researchers outside Africa we found researchers of various racial backgrounds but none that were ostensibly Black and therefore the Black/non-Black dichotomy was again unproblematic. In contrast, nationality was more complex and as a result we had to leave a few blanks. A caveat to the interpretation of affiliations is that many African scientists do doctoral study at non-African institutions that are then mentioned as affiliation, when, in fact, the person aspires to work in Africa (this is the case for two of the authors of the present paper; FG and MK). Evidently, it takes time to build a publication track record and the demography of upcoming cohorts of lion researchers may be different. The current student population in our own institutions suggests a possible recent increase in the number of Black Africans becoming lion researchers.

Nevertheless, our results show a distinct problematic pattern. The problem is not in the science, but in the availability of lion experts within range countries to contribute to lion conservation. An example of how bias pervades institutions is a screening of membership of the IUCN-affiliated African Lion Working Group. Members listed on their website (http://www.africanliongroup.org/ accessed 31/7/2018) include only 12% Black Africans, and there is a male to female 2:1 ratio in a membership of 112. There are political tensions in international meetings when expert groups advising African decision-makers are populated mainly by White men. The implications have been widely discussed (Karlsson et al., 2007; Mammides et al., 2016), we add that this is particularly relevant for lions—a species that is increasingly conservation dependent, leading to increased political interest (Bauer et al., 2018; Hodgetts et al., 2018). The present study is only an assessment of a few dimensions of identity, further study can look at the potential synergy between these dimensions and look at other dimensions like religion, sexual orientation, and socio-economic background.

There is no natural reason why Black or women researchers would be less able to do lion research and publish it. Black, and to a lesser degree women, underrepresentation in the authorship of lion publications could be a sign of discrimination and/or systemic bias. Underrepresentation in the community of conservation practitioners could well play a role (Mbaria and Ogada, 2016). Career choice is influenced by socio-economic conditions; less privileged groups tend to take economic prospects more into consideration (Jayachandran, 2015) and the economic prospects of a career in lion studies are rather limited; self-selection against this career may therefore play a role. For South Africa, the legacy of apartheid could explain bias in older cohorts of researchers. Another plausible explanation could be a possible "macho" culture among lion researchers, or the more positive attitude toward lions among non-Africans compared to communities living closer to them. Language barriers could be another issue; English has become the most common science language but it is not the first language for most Africans. Also, zoos, and wildlife information centers are rare in Africa, leading to less childhood exposure that could lead to increased interest in wildlife. These speculations, and possibly others remain to be tested.

However, such Individual-meritocratic have a limited explanatory potential; more importantly, there is a systemic problem (Nielsen, 2016). Scientific papers are primarily written by academic staff and graduate students, most of whom work in national higher education institutes that target their own citizens. The lion is a charismatic species, with an umbrella and keystone function, and it is therefore not surprising that many people around the world have been drawn to its study (Macdonald et al., 2015). In contrast, enrolment rates in tertiary education in Africa are the lowest in the world (Mohamedbhai, 2014), and from that smaller pool few academics with an interest in wildlife can afford the high cost of studying lions (i.e., relative to studying more abundant and less dangerous species). Many institutions worldwide have offered the opportunity to non-African scholars to study lions, but too few Africans appear to have had that opportunity.

Various instruments are available for affirmative action. One example is the use of research permits to pair foreign researchers with local counterparts. In Ethiopia for instance foreign individuals willing to study wildlife in Protected Areas are required to fund and involve local counterparts in any given study, and this typically includes formal University tuition and co-authorship of resulting scientific papers. Another example is the inclusion of parameters related to local participation in the evaluation criteria of grant-giving institutions, such as those practiced by the National Geographic Big Cats Initiative and the IUCN Save Our Species fund. Considerable development funding is also available for African science institutions generally, and for capacity building in the field of biodiversity conservation. However, these instruments have been used for many years, and have apparently not yet had the desired result.

We conclude that compliance with permitting and granting requirements are insufficient instruments to regulate equitable access to positions in the lion research community, or to maintain robust and consistent local participation in lion research and we call for additional efforts to involve Black, African, and women researchers in lion studies. Apart from the obvious benefit of brain gain for society in general, more inclusiveness can contribute to conservation effectiveness: having more lion researchers from lion range states would increase the voice and empowerment of important interest groups. In a sector already fraught with moral dilemmas (Duffy, 2016; Mollett and Kepe, 2018; Vucetich et al., 2018), this is an urgent shared responsibility.

AUTHOR CONTRIBUTIONS

HB and FG contributed to every aspect of the study. MK and CS-Z contributed to setting the research questions and edited the entire manuscript. LS assisted in collecting and organizing bibliometric data. All authors equitably contributed to the creation of this review and approve submission to Frontiers.

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Perceptions of Risk From Man-Eating Lions in Southeastern Tanzania

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Perceptions of risk are a critical component of understanding the human dimensions of human-wildlife conflict as perceptions greatly affect peoples' attitudes and behaviors toward wildlife. However, accurately assessing perceptions can be difficult since risk is often subjective and perceptions are affected by both emotions and experience. Lions attacked over 1,000 people in Tanzania between 1990 and 2007. We conducted questionnaire surveys to examine multiple aspects of risk perceptions in the areas with the highest incidence of lion attacks, focusing on three general questions: (1) how villagers perceive their overall risk of attack; (2) what factors influence risk perceptions; and, (3) what aspects of risk are perceived accurately. Overall, people overestimated their risk from lions: 53% of respondents felt they are very likely to be attacked while the actual risk is estimated at less than 1% over an average lifespan. Risk perceptions were correlated with gender, age, education, acres of cultivated land and number of livestock owned but not with previous experience with lion attacks in either the village or family or with sighting of lions or lion signs. Nevertheless, people were very aware of who was at relatively high risk and when and where risks were greatest. People also accurately assessed the risk from lions compared with mega-herbivores but not compared with other predatory species or with disease and famine, emphasizing the tendency for people to overestimate risks that are rare but elicit strong fears. This study highlights the value of using interdisciplinary techniques to examine human dimensions of human-lion conflict as risk perceptions and local knowledge can identify gaps in understanding that could improve conflict-prevention programs.

Keywords: human-wildlife conflict (HWC), risk perceptions and knowledge, human-dimensions, lions (*Panthera leo*), Tanzania

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INTRODUCTION

Lions attacked over 1,000 Tanzanians between 1990 and 2007 (Kushnir et al., 2010, 2014). The overwhelming majority of these cases were unprovoked, where lions entered human-dominated areas specifically to prey on people (Packer et al., 2005; Kushnir et al., 2010). Understanding how people perceive the risk of lion attacks is important to the development and design of an effective conflict-mitigation program because perceptions reveal how society and individuals view and respond to hazards (Tate et al., 2003). Peoples' perceptions affect attitudes and behaviors, making perceptions as important to consider as actual risk (Naughton-Treves, 1998; West and Parkhurst, 2002; Conforti and de Azevedo, 2003; Naughton-Treves and Treves, 2005; Gore et al., 2006; Baird et al., 2009; Thornton and Quinn, 2010). Perceptions also greatly influence support for conservation and the likelihood of retaliation toward species implicated in human-wildlife conflict (Conforti and de Azevedo, 2003) and are therefore critical for managing prevention efforts (Henderson et al., 2000; Kretser et al., 2009).

Numerous studies have examined perceptions and attitudes toward protected areas or wildlife (Manfredo et al., 1998; Bauer, 2003; Gadd, 2005; Lucherini and Merino, 2008) so as to determine how communities view conservation efforts. Other studies have specifically examined perceptions of problem animals or the damage they inflict on crops and livestock (McIvor and Conover, 1994; Naughton-Treves, 1997, 1998; Henderson et al., 2000; West and Parkhurst, 2002; Gillingham and Lee, 2003; Marker et al., 2003; Linkie et al., 2007; Kretser et al., 2009) or on human safety (Zinn and Pierce, 2002; Conforti and de Azevedo, 2003; Kleiven et al., 2004; Gore et al., 2006; Kaltenborn et al., 2006; Thornton and Quinn, 2010).

Many of these studies have either assessed overall perceptions (McIvor and Conover, 1994; Zinn and Pierce, 2002; Conforti and de Azevedo, 2003); (Marker et al., 2003; Gore et al., 2006; Kaltenborn et al., 2006; Kretser et al., 2009; Thornton and Quinn, 2010) or identified socioeconomic, demographic, cultural, or attitudinal factors that influence perceptions (Naughton-Treves, 1997; Zinn and Pierce, 2002; Conforti and de Azevedo, 2003; Kleiven et al., 2004; Gore et al., 2006; Kaltenborn et al., 2006; Kretser et al., 2009; Thornton and Quinn, 2010), while others have compared actual risk or damage to perceptions (Naughton-Treves, 1997, 1998; Henderson et al., 2000; Gillingham and Lee, 2003; Linkie et al., 2007). However, few studies have so far obtained a comprehensive picture of local knowledge and risk perceptions by examining not only overall perceptions but also examining the specific situations in which people feel at risk.

We investigated perceptions of man-eating lions in a situation where risks were real, fatal, and widespread. We examined risk perceptions to answer three questions: (1) How do people perceive their risk of being attacked by a lion? (2) How do past experience, demographics, socioeconomics and location affect perceptions? (3) How does perceived risk compare to documented attacks? Examining these aspects of risk provides a nuanced view of risk perceptions and local knowledge associated with lion attacks and contributes to the growing body of interdisciplinary research on human-lion conflict.

METHODS

Study Area

We worked in the two Tanzanian districts with the highest number of lion attacks: Rufiji and Lindi. These districts differ from each other in the abundance of wildlife and human activity patterns during lion attacks. Rufiji is near Selous Game Reserve and home to larger lion and herbivore populations than Lindi, which is not near any major protected area. In Rufiji, the majority of attacks occur at night in agricultural fields while victims are sleeping inside huts. In Lindi, the majority of attacks occur in the late evening, both in villages and agricultural fields, while victims are walking or conducting activities just outside their homes. Despite these contrasts, both districts experienced a major outbreak of lion attacks from 2001 to 2004. In both areas, most rural villagers are subsistence farmers who suffer considerable losses from nocturnal crop pests, particularly bush pigs (*Potamochoerus porcus*), which are important lion prey in these agricultural areas (Packer et al., 2005; Kushnir et al., 2010). The seasonality of lion attacks, outcome, and victim demographics were similar between districts Kushnir et al., 2010. Most attacks in Lindi and Rufiji occurred during the wet season, which corresponds to the harvest season, and the months with the most attacks were December, January, March, April, and May (when farmers remain in their fields to guard against nocturnal crop pests, Kushnir et al., 2010). Sixty-six percent of attacks on humans in Rufiji and Lindi were fatal ($N = 274$), 58% of victims were male, and 74% were adults.

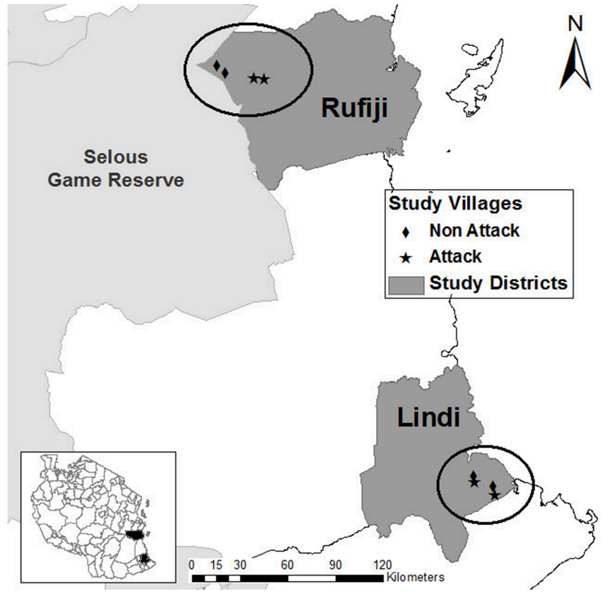

FIGURE 1 | Map of southeastern Tanzania with study districts in gray and study villages marked; circles denote areas with the highest concentration of attacks.

In each district, we conducted questionnaire-based interviews in the areas with the highest recorded concentration of attacks (**Figure 1**). Using attack locations obtained from district records verified through site visits to each village, we selected four villages in each study area: two with a history of attacks and two neighboring villages with no attacks. An "attack village" is a village that had attacks within its boundaries, which includes agricultural areas within its jurisdiction. A "non-attack village" is a village with no attacks from 1990 to 2007 as verified by both district records and site visits. In Rufiji, the two selected attack villages are between 18 and 29 km from the two selected non-attack villages. In Lindi, the two selected attack villages are between 4 and 6 km from the two selected non-attack villages.

Data Collection and Analysis

We conducted 128 questionnaire-based interviews with the help of a translator by randomly selecting 16 households from each village register and alternately selecting female and male household heads to ensure an even gender ratio; there was no indication that female household heads answered the surveys differently than males. Questionnaires included questions on demographics, socioeconomics, education, attack history in the family, sighting of lions and lion signs, and whether attacks increased or decreased over their lifetime.

Perceived Risk

We asked two prompted questions (where we gave interviewees a list of possible responses) to gauge perceived risk from lion attacks:

(1) Perceived likelihood-How likely do you think you are currently to be attacked by a lion (not at all, somewhat, very)?
(2) Worry-Are you worried about being attacked by a lion (not at all, a little, worried, very)?

Because of low responses for some categories for question 2, we grouped "not at all" and "a little" together and "worried"/"very" together for analysis.

With SPSS 16.0, we used the chi-square goodness-of-fit test and analysis of variance (ANOVA) to compare responses according to demographics (male/female, child/adult), socioeconomics, education, attack history in the family, sighting of lions and lion signs, and whether attacks increased or decreased over their lifetime.

Perceived Risk vs. Documented Attacks

We asked a number of questions about attack specifics (note that in Swahili, "risk" in the context of lion attacks translates to "danger"). Some of these were open-ended questions and others were prompted with possible answers provided:

- Do you think the following activity puts people at risk for lion attacks, if so how much risk (prompted—list of 11 activities: collecting firewood, getting water, collecting timber, fishing, walking alone during the day, walking alone when dark, guarding crops, sleeping in agricultural fields, using the toilet after dark, cooking outside after dark, sitting/resting outside after dark)?
- Where do you feel most at risk (prompted—village center, agricultural field, both, other/wild areas)?
- During which times of day do you feel most at risk (open-ended)?
- Who in your village do you think is most at risk of lion attacks (open-ended)?

Results from these questions were compared to details from documented attacks (whether those attacks were fatal or not). For activities, we categorized questionnaire and attack data into five categories that best aligned with each other. These five categories were: (1) activities outside the house including cooking outside after dark and sitting/resting outside after dark; (2) bathroom/bathing; (3) farming/guarding crops including sleeping in agricultural fields; (4) walking at any time of day; and (5) helping another victim. We chose to exclude five perceived risky activities that did not match with documented attack data because the level of details of attacks data was not as precise as the questionnaire. These were collecting firewood, getting water, collecting building materials, fishing, and collecting wild tubers. For times of day, we grouped responses for questionnaire and attack data into five categories (early morning, morning, afternoon, evening, night). We also grouped questionnaire responses for who is most at risk into child/adult and male/female to compare to documented attack data. Once data was categorized, we calculated the percent of responses in each category for questionnaire data and calculated the proportion of attacks in each category for documented attacks. We then plotted these results on a scatter plot (**Figure 2**).

To better understand perceived risk vs. documented attacks, we also asked respondents which threat poses the greatest risk: another wildlife/non-wildlife risk, a lion or both (comparison of risks). The additional wildlife included elephants (*Loxodonta Africana*), hippopotamus (*Hippopotamus amphibius*), buffalo (*Syncerus caffer*), crocodile (*Crocodylus niloticus*), leopard (*Panthera pardus*), and snake. Non-wildlife risks included drought, famine, malaria, and AIDS. We did not question people in Lindi about hippopotamus and crocodile because these species were not present in the area. We used chi-square to test for significant differences between lion-attack risk and other wildlife/non-wildlife risks and tested for differences in responses between attack- vs. non-attack villages and between people who had or had not had attacks in their family.

RESULTS

Perceived Risk

Overall, 53.2% thought they were very likely to be attacked, and 69.0% worried about being attacked. Given an average of 15.5 attacks per year in Rufiji and Lindi, a combined population of ∼450,000 people in the two districts, and an average lifespan in Tanzania of 55.9 years, a realistic estimate of an individual's lifetime chances of being attacked is well below 1%. There were no significant differences in response to the two perception questions (perceived likelihood, worry) between people living in an attack or non-attack village or between people with or without an attack in their family. There was also no significant difference in perceptions (perceived likelihood, worry) based on sightings of lions or lion signs in villages or agricultural fields, with one exception: people who saw lion signs in their village were more likely to be worried/very worried about attacks as compared with those that did not ($X^2 = 5.529, p < 0.05$). Males and females were equally worried about attacks, but females were more likely than males to think that they were not at all likely to be attacked ($X^2 = 10.123, p < 0.01$). People with more education (having completed Standard 5–7) were more worried ($X^2 = 9.978$, $p < 0.01$) about attacks and thought they were more likely to be attacked ($X^2 = 12.703, p < 0.05$) than those with less education (Standard 1–4) or no education at all. Although age did not have a significant effect on risk perceptions, people who thought attacks had increased were younger on average than those who thought that attacks had decreased ($F = 7.052$, $p < 0.01$).

Perceived Risk vs. Documented Attacks

Figure 2 shows risk-perception responses for locations, times, activities, age groups, and gender plotted against information from documented attacks. The closest points to the diagonal line

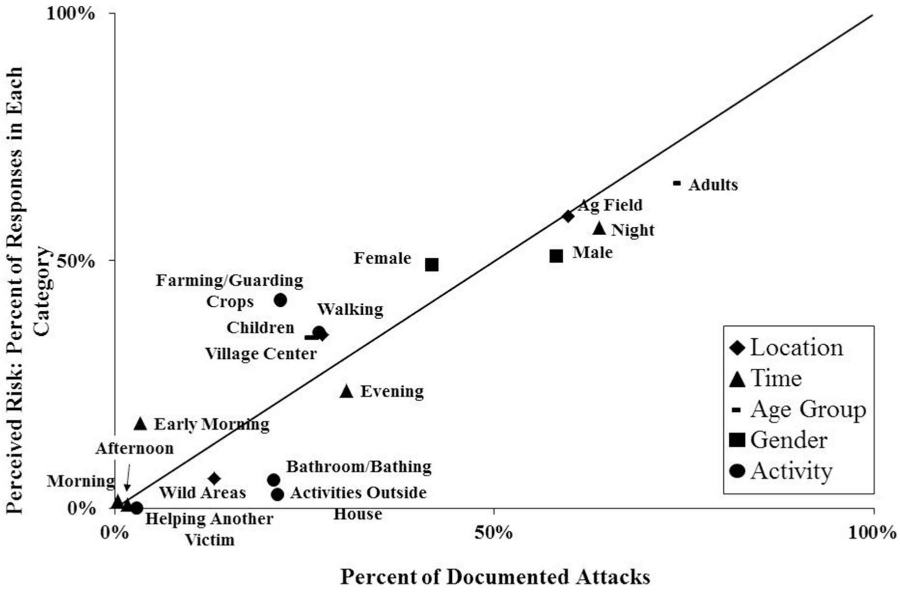

FIGURE 2 | Comparison of perceived risk vs. information from documented lion attacks. Risk-perception responses for locations, times, activities, age groups, and gender are plotted against information from documented attacks. The closest points to the diagonal line show the closest alignment between perceived and actual attack risks. Points below the line show when people underestimated the risks and points above the line show when people overestimated the risks.

show the closest alignment between perceived and actual attack risks. Points below the line show when people underestimated the risks and points above the line show when people overestimated the risks. Overall, perceptions aligned well with attack data as most points lie close to the diagonal. Perceptions diverged most for "activities"—people overestimated risks from farming and guarding crops and underestimated risks from using the toilet, bathing, and conducting activities just outside the house.

Overall, the majority of people considered lions to be more dangerous than elephants, hippopotamus, and buffalo and that crocodiles, leopards, and snakes were equally as dangerous as lions (**Figure 3**). Although most people said that risks from drought, famine, malaria, or AIDS were higher than risks from lions, a large proportion of villagers viewed these risks as equal to lion attacks (**Figure 3**). Significant differences were found between the three responses (lion, other, both equally) for all wildlife and non-wildlife risks except drought (elephant $X^2 = 37.434$, $p < 0.01$; hippo $X^2 = 16.000$, $p < 0.01$; buffalo $X^2 = 32.469$, $p < 0.01$; crocodile $X^2 = 14.281$, $p < 0.01$; leopard $X^2 = 30.333$, $p < 0.01$; snake $X^2 = 23.453$, $p < 0.01$; famine $X^2 = 8.172$, $p < 0.05$; malaria $X^2 = 15.559$, $p < 0.01$; AIDS $X^2 = 23.688$, $p < 0.01$). There were no significant differences in responses comparing lions to other wildlife or non-wildlife risks between attack- vs. non-attack villages or between persons who had or had not had attacks in their family.

DISCUSSION

Perceived Risk

A majority of individuals, even in villages that have never experienced attacks, felt that it was likely that a lion would attack them. Considering that over the course of an average lifespan people in Rufiji and Lindi districts have less than a 1% chance of being attacked, perceptions of risk appear to be considerably exaggerated.

An examination of the psychological literature on risk perceptions provides a framework for understanding why people are overly concerned about lion attacks. Numerous studies have discussed how emotions and feelings relate to risk perceptions and have shown that people often estimate risks on feelings rather than on an analytical risk assessment (Fischhoff et al., 1993; Slovic and Peters, 2006; Slovic et al., 2007). Studies have shown that people have an inflated perception of risk for involuntary and uncertain situations over which they have little control. The more sensational or vivid the consequences and the more feeling of dread associated with the risk, the higher people perceive their own risk to be (Johnson and Tversky, 1983; Slovic, 1987; Fischhoff et al., 1993; Tate et al., 2003; Slovic et al., 2007). One example is the tendency for people to overestimate their personal risks from an airplane crash; people focus so much on the outcome and nature of the event that they do not consider that it is unlikely to occur (Slovic and Peters, 2006). Lion attacks mirror risks like airplane crashes because even though lion attacks are rare, the consequences are high, the situations are terrifying, and attacks are completely out of peoples' control.

There was no relationship between an individual's previous experience with attacks, proximity to protected areas, and awareness of lions being present in villages and agricultural fields and his/her perceptions of risk, as defined by the two questions designed to measure perceived risk (perceived likelihood, worry). The only exception is that people who saw lions in their village were more worried about attacks.

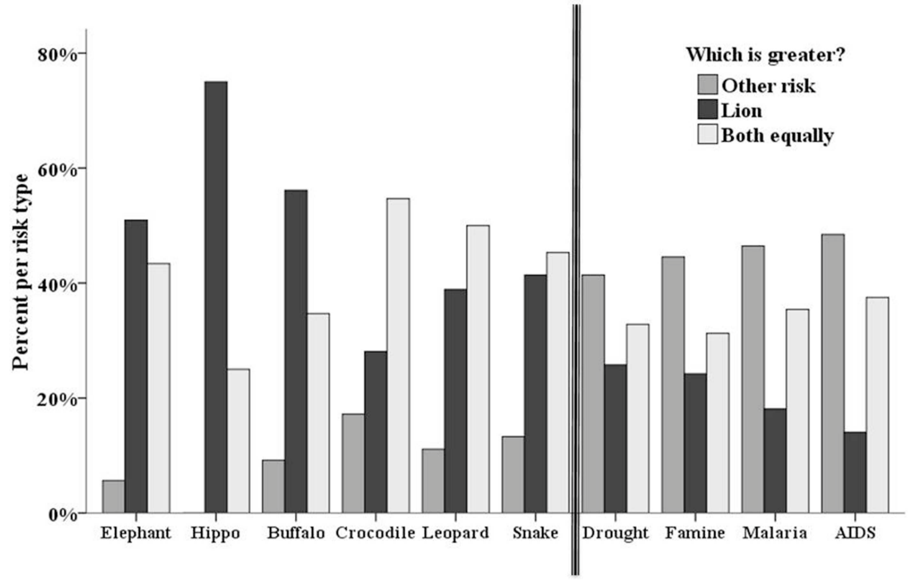

FIGURE 3 | Comparison of risk between lions and other wildlife **(Left)** and non-wildlife **(Right)** risks. Most people view the risk from lions to be greater than elephant, hippo, and buffalo and the same as crocodile, leopard, and snakes. Most people view drought, famine, malaria, and AIDS to be greater than the risk from lions.

Our findings contrast with earlier studies showing that people were more likely to report negative perceptions or higher levels of fear if they had experienced more economic loss, physical damage, or contact with wildlife (West and Parkhurst, 2002; Kleiven et al., 2004; Kretser et al., 2009; Thornton and Quinn, 2010). In our study, individuals with previous experience did not perceive their risk to be higher than individuals who lacked previous experience. This could be because the sensational nature of lion attacks on humans makes these events much easier to recall. According to the availability heuristic, this would lead people to consider themselves more likely to be attacked regardless of their personal experience. The availability heuristic states that "a person evaluates the frequency…or the probability of events by…the ease with which relevant instances come to mind" (Tversky and Kahneman, 1973). The extreme and uncontrollable nature of these events makes them easy to remember. Although there is almost no media publication of these events and little public transport between villages, most people can still recount stories of attacks that occurred multiple villages away.

Perceived Risk vs. Documented Attacks

People tend to be overly worried about attacks and to overestimate their likelihood of being attacked. This is not unusual, as many studies that compare perceived wildlife damage to actual damage have shown that people perceive loss to be worse than actual loss (Naughton-Treves, 1997, 1998; Gillingham and Lee, 2003). People also have a broader concept of risk than death or injury and often include outcomes such as psychological stress or loss in productivity in their risk assessments whereas experts generally consider risk only in terms of the likelihood of death or injury (Slovic, 1987). Perceptions may be amplified by people's inability to cope or lack of control over the situation (Naughton-Treves, 1997; Gillingham and Lee, 2003). For example, when people reflect on perceptions of crop damage they may not just be responding to direct crop loss but also the indirect cost of abandoning a field (Naughton-Treves and Treves, 2005). Additionally, there is always bias introduced by the questionnaire itself (Johnson and Tversky, 1983). Respondents knew that we were lion researchers and could have consequently exaggerated their concerns.

People are known to better identify relative risks even if they are unable to judge the true extent of a particular risk (Fischhoff et al., 1993; Slovic et al., 2007). By asking respondents about who might be most at risk (adult/child, female/male) and about the riskiest locations, activities and times, we found that the villagers' perceptions of at risk individuals, locations, activity, and times matched with actual risks, though some aspects of risk were more easily recognized than others. People generally did a good job assessing risk of specific locations, activities, and times, as well as the members of their community who were most at risk. However, compared with data from actual attacks, people tended to perceive higher risk from farming and guarding crops and lower risk from activities around the house, using the toilet and bathing. It is particularly striking that people most underestimated the risk around their home. This may indicate a false belief about safety of mundane activities, much like the tendency to underestimate the risk from driving while overestimating the risk from flying (Johnson and Tversky, 1983).

Comparing the risk of lion attacks to other dangers also highlighted a mismatch between perceptions and actual risk. People generally believe that lions are more dangerous than elephants, buffalo, and hippopotamus and that lions are equally as dangerous as crocodiles and leopards. Dr. Dennis Ikanda of the Tanzania Wildlife Research Institute surveyed district records in six districts in southeastern Tanzania and found that lions are responsible for 55% of all wildlife related deaths and injuries followed by crocodiles (13%), leopards (12%), hyenas (7%), elephant (6%), hippopotamus (5%), and buffalo (2%). These data show that people assess their risk from the mega-herbivores correctly, as elephants, hippopotamus, and buffalo do kill less people than lions. However, peoples' tendency to rate the risk of lions as equal to that of leopards and crocodiles illustrates the tendency to overestimate risk from situations that elicit dread and fear. People may not be responding to actual objective risk of death or injury but to a deep generalized fear of predatory species.

Most people viewed the danger from drought (41%), famine (45%), malaria (46%), and AIDS (48%) to exceed that from lions. However, a substantial number of people viewed these risks as being similar to lions (drought 33%; famine 31%; malaria 35%; AIDS 38%). According to the United Nations World Food Programme (2009), 58% of Tanzania's population lives on less than $1 a day, 44% are undernourished, and 38% of children under five are malnourished. The country is also plagued with irregular rainfall and 1.4 million people (3.4% of the total population) are living with HIV/AIDS (World Food Programme, 2009). Considering these statistics, it is remarkable that almost 40% of the interviewees perceived the risk from lion attacks to be the same as drought, famine, malaria, and AIDS when they had less than a 1% chance of being attacked by a lion over their lifetime. One explanation for this could be that though attacks are rare, the mortality rate from these attacks is very high (66%).

CONCLUSION

This research contributes to the growing body of interdisciplinary research on human-lion conflict by examining perceptions, an important human dimension of conflict that should be considered when designing policy and program interventions. Consistent with the literature on risk perceptions of other spectacular though rare events, people in Rufiji and Lindi districts overestimated their likelihood of being attacked by a lion. However, when questioned about specifics, people were very aware of where and when they were most at risk. Consistent with the availability heuristic, the majority of the population was presumably concerned about attacks because details were easy to recall. Knowing this, management officials could potentially implement prevention efforts just as easily in communities with a history of attacks as those without attacks. Heightened perception of risk and easy recall of human-wildlife conflict events could make people more likely to take preventative action that can save lives and livelihoods and forestall retaliation against threatened wildlife species.

Beyond overall perception of risk, it is critical to identify the specific locations and activities where people feel most at risk. This information can help conservation practitioners target conflict prevention measures and community education programs. For example, in Rufiji and Lindi, people underestimate their attack risk near their homes and may more readily take preventative actions in agricultural fields or walking in the village periphery. This means education must not only focus on risk in areas outside of village centers but also closest to peoples' homes.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Institutional Review Board (IRB) at the University of Minnesota. The research involved minimal risk to subjects, thus, the IRB approved a waiver of informed consent for the project.

AUTHOR CONTRIBUTIONS

HK designed and conducted the field research, analyzed the data, interpreted the result, and wrote and the manuscript. CP provided input into study design, data analysis, and interpretation of results and provided feedback on the manuscript.

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Apparent Competition, Lion Predation, and Managed Livestock Grazing: Can Conservation Value Be Enhanced?

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Predator restorations often result in apparent competition, where co-occurring prey populations experience asymmetric predation pressure driven by predator preferences. In many rangeland ecosystems, livestock share the landscape with wildlife, including ungulates and the large carnivores that consume them. We examined whether apparent competition reorganized prey communities following restoration of lions (*Panthera leo*) to a savanna ecosystem, and whether and how livestock management could alter this indirect interaction between lions and their prey. Three lines of evidence supported the hypothesis that Jackson's hartebeest (*Alcelaphus bucelaphus lelwel*; an ungulate of conservation concern) are suppressed via lion-mediated apparent competition. First, hartebeest exhibited an Allee effect where they were exposed to lions, but displayed negative density-dependent population growth where they were protected from lions. Second, spatial overlap between plains zebra (*Equus burchelli*; the primary prey of lions) and hartebeest further exacerbated lion predation on hartebeest. Finally, hartebeest were killed selectively by lions, whereas zebra were killed by lions in proportion to their abundance. We then tested whether glades [nutrient-rich hotspots created by abandoned cattle (*Bos indicus*) corrals] could be used to manipulate top-down control of hartebeest via their influence on the spatial distribution of zebra. Zebra aggregated at glades, and survival of hartebeest increased with increasing distance from glades, suggesting that corrals may be placed on the landscape away from hartebeest to create spatial refuges from lions. Our findings demonstrate how informed placement of livestock corrals can be used to manipulate the spatial distribution of primary prey (zebra), thereby reducing apparent competition suffered by hartebeest. Our work further provides an example of how integrating apparent competition theory with proactive livestock management can improve conservation efforts in multiple-use landscapes.

Keywords: African savanna, Allee effect, glade, human-occupied landscape, refuge, refuge-mediated apparent competition, wildlife–livestock interactions, hartebeest

INTRODUCTION

The restoration of large carnivores can infuse optimism into conservation efforts that, historically, have been characterized by reactive, stopgap measures (Chapron et al., 2014; Wolf and Ripple, 2018). In the aftermath of such predator restoration, however, prey species often exhibit marked changes in numbers and behavior, such that composition and relative abundance of post-restoration prey communities may bear only slight resemblance to that of communities prior to predator extirpation (Lovari et al., 2009; DeCesare et al., 2010). Differences in carnivore-extirpated vs. carnivore-restored communities of prey often are attributed to apparent competition, in which preferences for prey by large carnivores lead to differences in the degree to which prey—some which are themselves conservation concerns—are suppressed via top-down control (Holt, 1977; Holt and Kotler, 1987; see DeCesare et al., 2010 for a review of cases in which apparent competition presents challenges for conservation; Holt and Bonsall, 2017).

Regardless of the mechanism by which they arise, prey preferences often result in secondary (less common) prey incurring greater risk of predation in proximity to primary prey. Secondary prey may decline while primary prey subsidize large carnivores, such that abundances of large carnivores and secondary prey are decoupled, driving the latter to rarity or even local extinction (e.g., Schmidt, 2004; Angulo et al., 2007; Hervieux et al., 2014; Serrouya et al., 2015; Chan et al., 2017). The likelihood that apparent competition generates these predator-mediated Allee effects—the decrease in population growth at small population sizes, (Allee et al., 1949; Courchamp et al., 1999)—is greatest when large carnivores are restored after lengthy periods of extirpation, during which environmental conditions have changed, and prey abundance has increased (but see Berger et al., 2001; Ford and Goheen, 2015; Stier et al., 2016). Against the backdrop of shifted environmental conditions, effects of large carnivores can be stronger than expected, presenting a conservation challenge to species of secondary prey.

The factors that drive prey preferences—and thus predispose secondary prey to high rates of predation—include differential resilience of primary vs. secondary prey to predation, and differential space use between primary and secondary prey (DeCesare et al., 2010; Wittmer et al., 2013). This second feature of predator-prey dynamics can result in "gradients of consumption" (in which risk of predation varies monotonically and directionally; Orrock et al., 2008), creating refuges where encounters between large carnivores and their secondary prey are infrequent. In giving secondary prey a potential foothold for positive population growth, refuges are one of the few ways shown to negate predation-mediated Allee effects in nature, thereby providing a potential tool to ameliorate apparent competition (Sinclair et al., 1998).

African savannas hold promise and conservation importance for understanding how spatial refugia might be used to reduce apparent competition stemming from predator restoration. Almost invariably, communities of savanna ungulates are dominated by a single species that typically constitutes the primary prey for large carnivores, yet achieves sufficiently high abundances to escape top-down control. In contrast, populations of less abundant species (i.e., secondary prey) tend to be suppressed by large carnivores, thus creating strong potential for apparent competition (e.g., Sinclair, 1985; Harrington et al., 1999; Owen-Smith and Mason, 2005; Georgiadis et al., 2007a; Chirima et al., 2012). Ranching occurs alongside wildlife in many African savannas, and landscapes in these human-occupied systems bear the imprint of livestock production in the form of glades: nutrient hotspots that attract wild ungulates and are derived from abandoned corrals or "bomas" (Augustine and McNaughton, 2006; Porensky and Veblen, 2015). Because livelihoods based purely on livestock production are becoming less reliably profitable, a changing mindset—to balance pastoralism with tourism, and potentially wildlife conservation—is gaining traction in many areas (Prins et al., 2000; Odadi et al., 2011; Keesing et al., 2018). Viewing large predators consistently ranks as a top priority among tourists, potentially leading to financial benefits in ecotourism ventures (Lindsey et al., 2007). Restoring large predators along with diverse assemblages of wild ungulates may be key to economic viability in these regions (Cousins et al., 2008; Stein et al., 2010).

The goals of our study were 2-fold. First, we sought to test the hypothesis of apparent competition (**Figure 1**) in Laikipia County, Kenya. Here, multiple species of wild ungulates—most notably Jackson's hartebeest (*Alcelaphus buselaphus lelwel*; hereafter simply "hartebeest")—have experienced recent declines following lion (*Panthera leo*) restoration in the late 1980s (Georgiadis et al., 2007b; Ng'weno et al., 2017). Restoration of lions has resulted from greater tolerance by ranch managers following decades of control via shooting and poisoning; however, declines in hartebeest populations are increasingly viewed as a particular conservation concern, leading some ranch managers to consider re-implementing lethal control of lions (Georgiadis et al., 2007b J. R. Goheen pers comm with Laikipia ranchers). Indeed, the impact of lion predation is sufficient to shift population growth of hartebeest from positive to negative (Ng'weno et al., 2017). In contrast to hartebeest and other declining species, populations of plains zebra (*Equus quagga*; hereafter simply "zebra")—the primary prey for lions in Laikipia—fluctuate in response to rainfall and density (Georgiadis et al., 2007a), but have not decreased with recovering lion numbers (Georgiadis, 2011; O'Brien et al., 2018). Consequently, we hypothesized that zebra populations suppressed those of hartebeest via apparent competition.

After assessing the hypothesis of apparent competition, we then tested whether livestock management could be used to manipulate the spatial distribution of predation risk to hartebeest, potentially enhancing coexistence of lions and their prey (and potentially removing a reason to lethally control lions). Under the hypothesis of apparent competition, we expected hartebeest in proximity to zebra to incur higher rates of predation. Because zebra (but not hartebeest) are attracted to glades (Veblen and Young, 2010; Augustine et al., 2011), we sought to quantify whether spatial separation between primary (zebra) and secondary (hartebeest) prey, driven by glade location, moderated apparent competition between zebra and hartebeest. Specifically, we predicted that (1) hartebeest occurring in areas

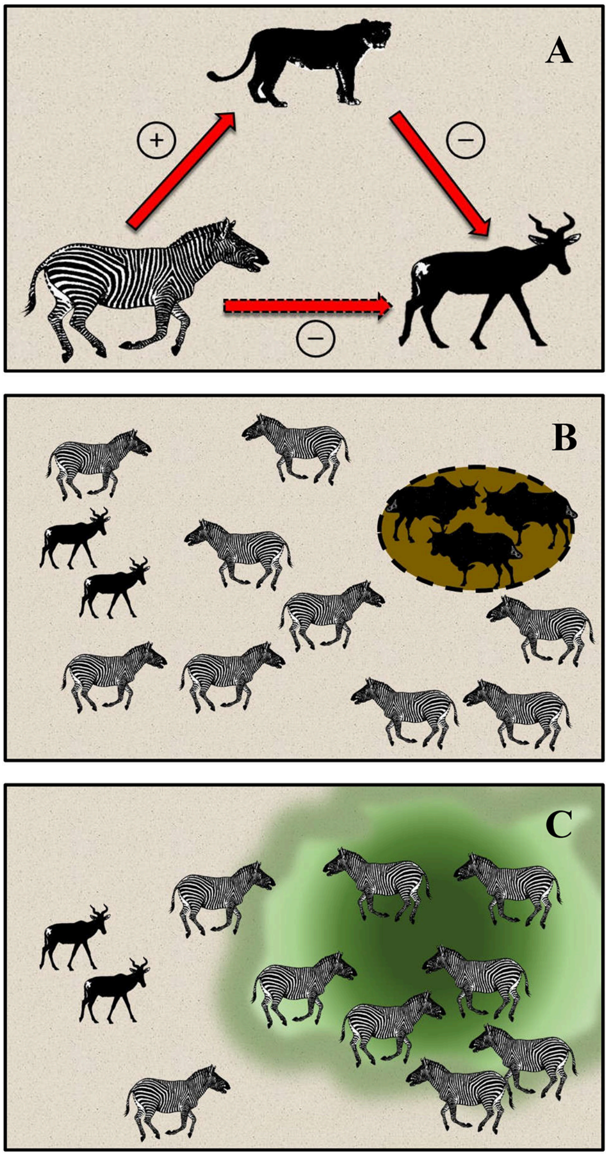

FIGURE 1 | Hypothesized species interactions among lions, plains zebra, Jackson's hartebeest, and cattle in Laikipia, Kenya. **(A)** The hypothesis of apparent competition. Zebra populations are controlled bottom-up by rainfall, are the primary prey of lions, and support a growing population of lions since the cessation of lethal control in the late-1980s. Although they are less abundant than zebra, hartebeest are selectively killed by lions and are controlled top-down, such that hartebeest incur negative, indirect impacts from zebra via lions. **(B)** Cattle are corralled overnight in bomas where they deposit dung and urine for a period of ca. 1 month. **(C)** After abandonment, dung and urine break down over the course of 2–3 years, creating nutrient-rich forage in glades where zebra aggregate, but not hartebeest. This creates spatial separation between zebra and hartebeest, and potentially a refuge from predation if lions target hunting activity toward areas where zebra are abundant.

of high zebra density would incur greater risk of predation from lions; and (2) hartebeest survival would increase with increasing distance from glades. In the event that predation risk to hartebeest could be manipulated via spatial separation of hartebeest and zebra, this would provide a potential solution through which hartebeest numbers could be bolstered without lethal control of lions.

MATERIALS AND METHODS

Study Area

We conducted fieldwork in Laikipia County, Kenya, at Ol Pejeta Conservancy (N0° 00′-S0° 02′; E36° 44′-36° 59′). Ol Pejeta is a 364-km^2 savanna managed jointly for wildlife conservation and Boran cattle (*Bos indicus*). With annual rainfall of 900 mm (Wahungu et al., 2011), Ol Pejeta is characterized by a wooded grassland dominated by the whistling-thorn tree, *Acacia drepanolobium*. The understory is dominated by the grasses *Themeda triandra, Pennisetum straminiem, P. mezianum* and *Brachiaria lachnatha*. Zebra are the most common wild ungulate at Ol Pejeta (individuals/km^2 = 11.55 ± 1.22 SEM); other wild ungulates consumed by lions include buffalo (*Syncerus cafer*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Nanger granti*), hartebeest, impala (*Aepyceros melampus*), oryx (*Oryx gazella*), Thomson's gazelle (*Eudorcas thomsonii*), warthog (*Phacochoerus africanus*), and waterbuck (*Kobus ellipsiprymnus*). In addition to lions, large (>10 kg) carnivores include black-backed jackal (*Canis mesomelas*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), and spotted hyena (*Crocuta crocuta*).

Estimation of Hartebeest Abundance and Population Growth

Between 2009 and 2015, we estimated hartebeest population growth and size within two zones under different management regimes: (1) a 294-km^2 area in which cattle production occurred alongside wildlife with the full complement of large carnivores (hereafter "control"); and (2) a 32-km^2 lion exclusion zone (hereafter "lion exclusion"), constructed with the intent of boosting numbers of declining ungulates, primarily hartebeest. The exclusion zone was demarcated from the adjacent control zone by a 2.5-m tall solar powered electrified (6,000–7,000-volt) fence with nine strands spaced 0.2 m apart. The fence was fortified with chain-link 1.50 m above and 0.60 m beneath the ground, preventing lion incursion but remaining permeable to other large carnivores (Ng'weno et al., 2017). Stocking rates were maintained at equal densities of 20 cattle /km^2 in both zones. From 2009 to 2015, we conducted twice-monthly drive transects for hartebeest in both zones. During each sampling period, we systematically drove 17 (4–13 km) transects (12 in the control zone, 5 in the lion exclusion zone), based on a predetermined random starting point. We conducted surveys during 07:00–11:00 h, driving at a maximum speed of 10–15 km/h with two trained observers. At each hartebeest sighting, we recorded the group size and the distance and compass bearing to the group with binoculars and laser rangefinders following standard distance sampling methods (Buckland et al., 2015).

Hartebeest maintain small groups (Kingdon et al., 2013; x = 16 in this study), characterized by strong dominance hierarchies among females. Groups are relative sedentary and defend small (<5 km^2) territories against conspecifics; as a result, we were able to identify and track 179 unique individuals in 11 distinct groups over the latter 4 years of our study (2012–2015; see "*Hartebeest survivorship and refugia analysis*" below; Ng'weno et al., 2017).

Typically, apparent competition is characterized by one or more species of secondary prey that exhibit an Allee effect (Allee et al., 1949; Courchamp et al., 1999; Stephens et al., 1999). To test for an Allee effect, we calculated the instantaneous rates of increase (r) for each zone (control and lion exclusion) as $r = \frac{N_{i+1}-N_i}{t_{i+1}-t_i}$, where N is the estimate of population size from the ith survey at time t (Sinclair et al., 1998). For hartebeest populations in both zones, we related population size to r, and determined goodness-of-fit of curves from regression analysis (Zar, 2010).

Prey Selectivity of Lions

From 2012 to 2015, we used distance-sampling methods to conduct quarterly drive transects to estimate the abundance of 11 species of ungulates killed and consumed by lions (hereafter "lion prey"). We systematically drove the 12 transects in the control zone while two observers recorded species, group size, sighting distance, and bearing to all lion prey sighted along transects. To evaluate whether lions killed prey in proportion to their availability, we fit 5 female lions with Global Positioning System (GPS) collars (Vectronic Aerospace GmbH, Berlin, Germany) from March to May 2014. These lions belonged to 5 different prides, which collectively accounted for ca. 80% of lions on Ol Pejeta (Ng'weno et al.; Ng'weno, 2017 in revision). Overlap between home ranges of prides was minimal (1–12%) throughout the course of our study (Ng'weno et al. in revision). All procedures were conducted with a veterinary team under the authority of the Kenya Wildlife Service.

From March 2014 to December 2015, we located lion kills from clustered locations of lions with GPS collars using an algorithm adapted from Knopff et al. (2009). Between August 2014 and December 2015, there were 246 instances in which prey carcasses were found to have been killed by lions (Ng'weno et al.; Ng'weno, 2017 in revision). We then used Jacobs' index (Jacobs, 1974; Hayward and Kerley, 2005) to quantify seasonal selectivity for each of 11 species of lion prey, $D = \frac{r-p}{2r-2rp}$ where r is the proportion of a given species among all kills, and p is its proportional abundance in the total prey population. Jacobs's index is bounded between −1 (highly avoided) and 1 (highly selected). Selectivity indices were calculated for each of the 11 species of lion prey, using carcasses from GPS clusters and estimates of prey abundance collected from August 2014 to December 2015.

Zebra Density and Risk of Predation to Hartebeest

To quantify the impact of primary prey (zebra) density on lion predation of hartebeest, we generated spatially-explicit density surfaces for zebra using resource selection functions (RSF) in a use-availability design (Manly et al., 2002). We constructed a minimum convex polygon (MCP) around all zebra herd locations from the quarterly surveys, and paired these with an equal number of random locations (n = 2,450) to achieve a 1:1 ratio of used to available locations. We then used a Rapideye satellite image (Digital Globe, Longmont, Co, USA) from May 2013 with 5–m spatial resolution to perform an unsupervised classification through isoclustering and maximum likelihood to group pixels with similar spectral reflectance into identify three habitat types: dense bushland (characterized by >50% cover of the tree *Euclea divinorium*), open bushland (characterized by 10–30% cover of the tree *A. drepanolobium*), and open grassland (characterized by <5% tree cover) (Birkett, 2002; Goheen and Palmer, 2010; Ng'weno et al., 2017). Following assignment of pixels, we ground-truthed our classification using 50–100 points in each habitat type. We performed all image processing using ERDAS Imagine, version 14 (Hexagonal Geospatial, Madison, Alabama) and ArcGIS version 10.3 (ESRI, Redlands, California).

Using the Euclidian distance and spatial join tools in ArcGIS 10.3, we extracted distances to the nearest water source and the nearest glade for each used and available location in each survey-specific zebra MCP. We related locations of zebra herds to habitat type, distance to nearest water source, and distance to nearest glade in 30 × 30 m pixels. Collinearity between habitat variables (habitat type, distance to water, distance to glade) was minimal (r < 0.50; P > 0.20 for all possible pairwise combinations).

We used logistic regression to estimate RSF coefficients, with selection for or avoidance of a habitat variable indicated by coefficients >1.0 and < 1.0, respectively (Manly et al., 2002). We used the resultant coefficients to generate a zebra RSF, rescaled to create 16 continuous surfaces (one for each of the 16 quarterly surveys conducted during 2012–2015) with 30 × 30 m pixel values ranging between 0 (strongest avoidance) and 1 (strongest selection), divided into 5 bins of equal width following Morris et al. (2016). The first bin corresponded to the lowest probability of zebra selection (0.00–0.20) and the fifth bin corresponded to the highest probability of zebra selection (0.81–1.00). We combined survey-specific zebra densities with survey-specific RSFs to create spatially-explicit density estimates for zebra in each survey, which we validated independently using camera-trap grids (Appendix 1; Ng'weno et al.; Ng'weno, 2017 in revision). See Boyce et al. (2016) for a similar approach in using RSFs to estimate spatial variation in abundance.

Finally, we superimposed locations of hartebeest killed by lions (n = 27) obtained from GPS clusters to the spatially-explicit zebra density surface with which it was most closely associated in time. We used Chi-squared tests to assess differences in the proportion of hartebeest kills occurring within the highest (> 9.60 zebra/km^2) and lowest (<2.40 zebra/km^2) areas of estimated zebra density.

Glade Creation Experiment and Hartebeest Survival

For the period 2012 to 2015, we calculated survival rates of individual hartebeest, with biological years starting 1 October and ending 31 September of each subsequent year (corresponding to birth peaks). Survival of female adults, sub-adults, and calves collectively accounts for >70% of the variation in population growth of hartebeest at Ol Pejeta (Ng'weno et al., 2017). During our twice-monthly sight-resight drive surveys (see "*Estimation* *of hartebeest abundance and population growth*" above), we monitored survival of 179 adults, sub-adults, and calves within 11 groups in the control zone. Because they defend small (<5 km^2) territories, we were able to use unique marks (i.e., ear nicks, horn size, and shape, scars) to monitor survival through repeated surveys (Ng'weno et al., 2017). Because female hartebeest exhibit high site fidelity (Gosling, 1974), we equated disappearance with death. There were no instances in which an individual classified as "dead" during a particular survey was detected subsequently. Survival rates were calculated using the R package "survival" version 2.41-3 (Therneau, 2017).

Over the course of ∼3 years, abandoned boma sites transition into glades and become attractive to zebra because of high biomass of *Cynodon* and *Pennisetum* grasses (Veblen and Young, 2010; Porensky, 2011; Veblen, 2012). Glades vary in their sizes and shapes; we therefore selected and restricted our analyses to 37 glades derived from bomas that we established in 2009 and 2010 (**Figure 4**). Nineteen of these bomas were established along the edges of open plains as part of an experiment to understand how glades give rise to various edge effects (Porensky and Veblen, 2015; Porensky and Young, 2016). Subsequently, 18 additional bomas were established in the middle of open plains to further quantify resource selection of zebra and survival of hartebeest. All bomas were 17.2 ± 0.8 m SEM in diameter, and used by ∼200 cattle for 1 month.

To assess the influence of boma-derived glades on survival rates of hartebeest, we constructed 95% isopleths using fixed kernel density estimation to create utilization distributions (UD's), with least squares cross validation and a smoothing factor of 1,000 using R package "adehabitatHR" version 1.8.18 (Seaman and Powell, 1996; Powell, 2000; Calenge, 2006). We then overlaid glades onto hartebeest territories, and calculated the distance from the centroid of each sighting of each hartebeest group to the nearest glade.

To assess whether glades reduced hartebeest survival in accord with the hypothesis of apparent competition, we fit two Cox proportional hazards (PH) models (Cox, 1972) to a dataset on hartebeest mortality derived from two sources: the 27 kills that we detected from collared lion GPS clusters from May 2014 to December 2015, and 101 additional events in which individuals disappeared (and were equated with mortality events) from sight-resight surveys from January 2012 to May 2014. For every individual killed that was detected from GPS clusters, we noted absences through sight-resight surveys. No individuals disappeared in our sight-resight surveys between May 2014 and December 2015 that we did not independently discover through GPS kill-site clusters. In other words, 100% of the hartebeest in our study were killed by lions. Through the first PH model, we quantified how risk of mortality varied with the (categorical) presence of a glade within home ranges of hartebeest groups. Here, we assessed whether glade presence altered the hazard ratio (probability of death) of individual hartebeest over the course of 3 years. Because individuals belonged to one of 11 groups, and because groups were relatively sedentary over the course of our study, we incorporated frailties (random effects) associated with group identity (Fox et al., 2006; Goheen et al., 2010) using R package "frailtypack" version 2.12-3 (Rondeau et al., 2012). Finding random effects of group membership negligible (see "*Results*" below), we fit a second PH model in which distance to glade edge was used as a continuous covariate to explain hartebeest mortality (we did not attempt to combine frailties and continuous covariates within a single PH model, because both are challenging to integrate into PH models simultaneously; Lopez de Ullibarri et al., 2012). In calculating distances, we used the midpoint of the pair of sight-resight survey locations where an individual was last sighted with its group, and where it was first noted to have disappeared. All analyses were undertaken in R version 3.4.0 (R Development Core Team, 2017).

RESULTS

Exclusion of lions was sufficient to shift population growth of hartebeest from negative to positive, consistent with a lion-mediated Allee effect (**Figure 2**). In the lion exclusion zone, population growth of hartebeest displayed a classic signal of negative density-dependence (**Figure 2**). In contrast, population growth of hartebeest increased with increasing population size in the control zone (**Figure 2**). Of the 11 species of ungulates killed by lions, zebra were consumed most frequently (40% of kills, $n = 98$) followed by warthog (15% of kills; $n = 37$), buffalo (14% of kills; $n = 35$), impala (14% of kills; $n = 34$), and hartebeest (13% of kills; $n = 27$). Lions consumed hartebeest and warthog disproportionately more than expected based on their abundance in both seasons, and zebra were consumed as frequently as expected based on their abundance in both seasons (**Figure 3**). The remaining 8 species of ungulates consumed by lions were avoided in at least one, and sometimes both, of the two seasons (**Figure 3**).

Zebra aggregated in and around glades (distance to glade: $\beta = -2.30 \pm 0.41$ SEM, $Z = -5.61$, $P < 0.0001$), and the best supported RSF for zebra contained terms for distance to glade, distance to dense woodland, and distance to water (**Supplemental Table 1**). Hartebeest died more frequently than expected in areas of high zebra abundance ($\chi^2_4 = 42$, $P < 0.001$; **Figure 4**). Consequently, and after nearly 3 years, survival among hartebeest lacking glades in their territories was over twice as high compared to those individuals whose territories contained glades ($\beta = 2.35 \pm 0.19$ SEM, hazard ratio = 2.10, $P < 0.001$; **Figure 5**). Incorporating frailty terms to account for heterogeneity in survival among hartebeest groups did not significantly reduce PH model deviance ($\chi^2_{10} = 11$, $P > 0.10$). Using distance from the nearest glade's edge, we found evidence for spatial refugia around 600 m: with every 100 m closer to a glade, hartebeest incurred a roughly 15% greater chance of mortality ($\beta = 0.14 \pm 0.012$ SEM, hazard ratio = 1.15, $P < 0.001$).

DISCUSSION

Multiple lines of evidence suggest that, over the course of 7 years, hartebeest were limited by apparent competition triggered by the restoration of lions on Ol Pejeta Conservancy. Lion exclusion erased Allee effects, and resulted in negative density dependence in hartebeest at populations below around 80 (**Figure 2**). Lions

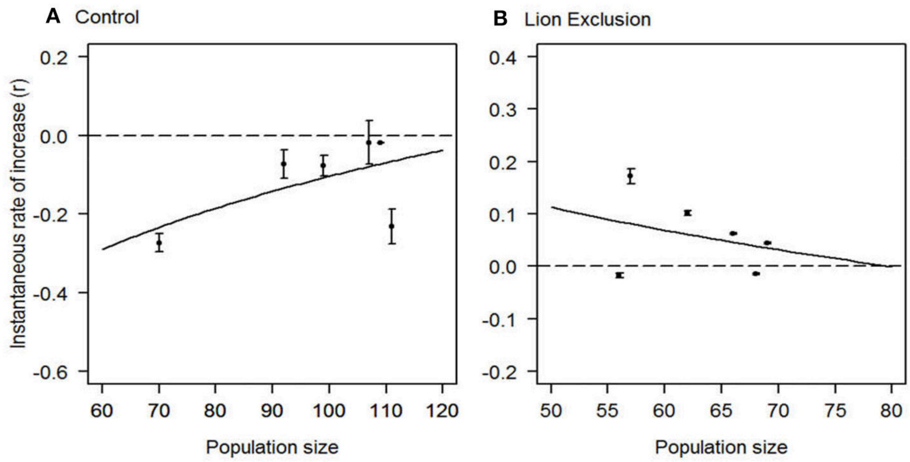

FIGURE 2 | A lion-mediated Allee effect in hartebeest populations. Correlations between annual instantaneous rates of increase (*r*) for hartebeest populations in **(A)** control zones exposed to lion predation ($r = 0.37 * \ln(\text{population size}) - 1.79$); and **(B)** lion exclusion zones [$r = -0.241 * \ln(\text{population size}) + 1.06$] from 2009 to 2015. Error bars are 95% confidence intervals based on sampling variance of population estimates.

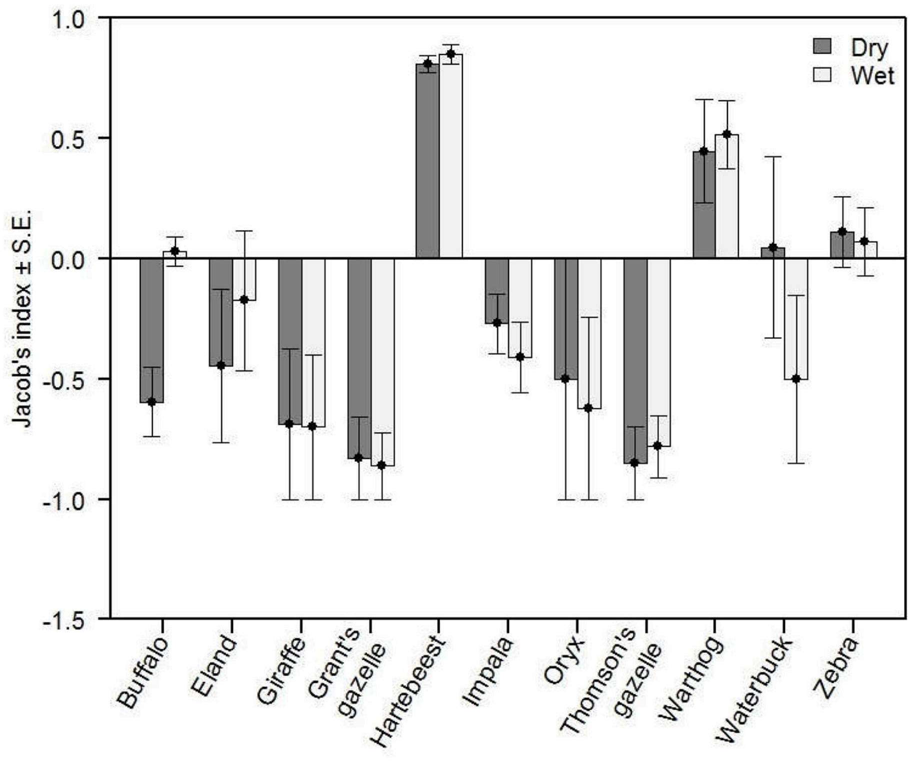

FIGURE 3 | Selectivity indices (Jacobs' index of selection) for 11 species of ungulates by five lion prides during wet and dry seasons. Hartebeest (and warthog, to a lesser extent) are selected regardless of season, while zebra are killed in proportion to their abundance in both seasons. All other species of ungulates are avoided during at least one season. Error bars represent standard errors.

consumed mostly zebra, and in proportion to their abundance, but selectively killed hartebeest (**Figure 3**). Zebra aggregated in and near glades, and mortality risk to hartebeest roughly doubled when glades occurred within hartebeest territories (**Figure 5**). Because ca. 80% of hartebeest mortality at Ol Pejeta is due to predation by lions (Ng'weno et al. in review), we attribute this change in patterns of mortality to a "gradient of consumption" (Orrock et al., 2008) that reduces survival of hartebeest in proximity to glades, and creates spatial refugia from lion predation beyond about 600 m from glades. Importantly,

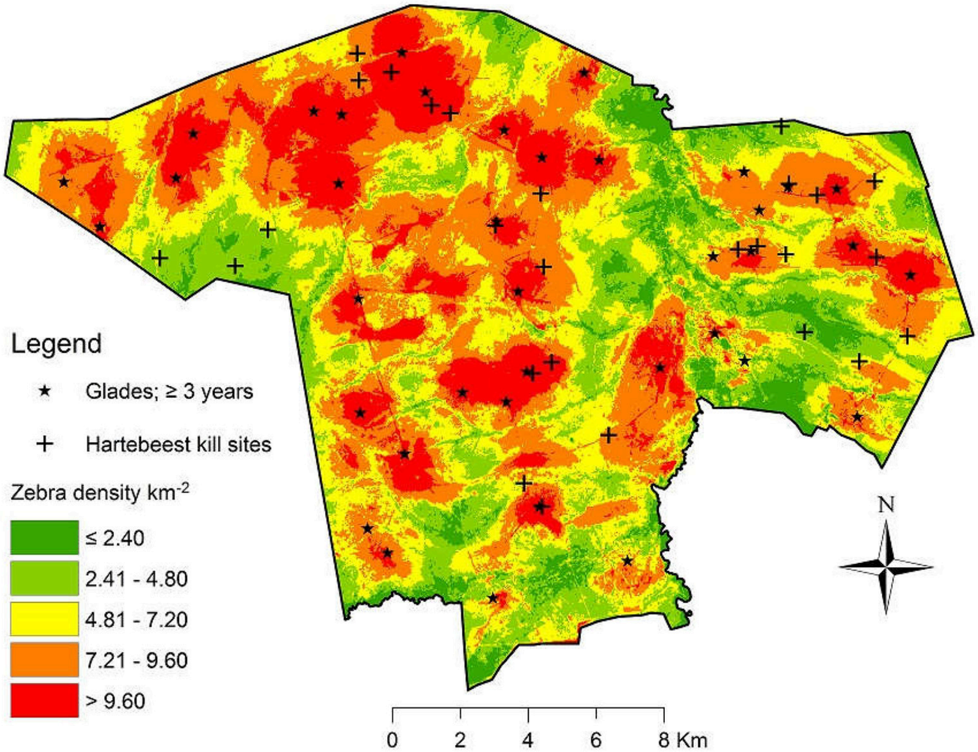

FIGURE 4 | Map with the locations of glades (≥3 years of age, $n = 37$) and hartebeest kill sites ($n = 27$) superimposed on a density surface for plains zebra. Estimates of zebra density (individuals/km^2) transitions from high (red) to low (green), and is driven largely by glade location.

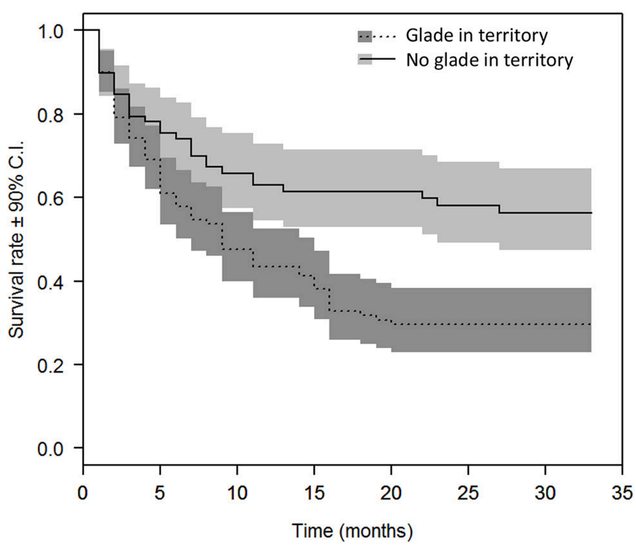

FIGURE 5 | Survival rates and 90% confidence intervals from Cox proportional hazards models for hartebeest with territories containing vs. lacking glades. Survival for hartebeest with territories containing glades is roughly half that of those whose territories lack glades.

we did not study the mechanism underlying the Allee effect we observed, which reduces our ability to predict future hartebeest population trends at Ol Pejeta, or characterize the generality of our observations to other settings. Across vertebrates, Allee effects have been variously attributed to loss of genetic variability, reduced social facilitation, and difficulty finding mates. In our system, the effect appears linked to lion predation specifically: the higher preference of lions for hartebeest, or a reduction in shared vigilance in hartebeest herds. Lions may search for hartebeest groups, which tend to be in predictable places, and expend disproportionate effort to kill a hartebeest, once a group is detected.

Instances where apparent competition has been implicated in limiting ungulate populations are becoming numerous, including bighorn sheep (*Ovis canadensis*), mountain caribou (*Rangifer tarandus*), huemul (*Hippocamelus bisulcus*), and roan antelope (*Hippotragus equinus*; Harrington et al., 1999; DeCesare et al., 2010; McLellan et al., 2010; Wittmer et al., 2013; but see O'Brien et al., 2018 for an example contrary to the hypothesis of apparent competition involving Grevy's zebra [*E. grevyi*] in Laikipia). In our study system, spatial separation between zebra and hartebeest improved survival rates of hartebeest, probably by reducing encounters with lions hunting in areas with high zebra densities (Ng'weno et al.;Ng'weno, 2017 in revision; see also Palmer et al., 2003; Forrester and Steele, 2004). Strategic placement of glades therefore offers a promising approach to creating refuges for hartebeest and perhaps other species of secondary prey. By siting bomas away from hartebeest, the establishment of glades was used to move zebras (and presumably lions) away from hartebeest territories.

The creation of spatial refugia and the reduction of primary prey alongside predators have previously been effective in releasing secondary prey from apparent competition in the past (Sinclair et al., 1998; Wittmer et al., 2013). Only the former is logistically feasible in our study system. Lions are Red-listed as Vulnerable by the IUCN and are at least as high a conservation priority as Jackson's hartebeest. At first glance, elimination of glades through reduction of cattle production might be considered another option for hartebeest conservation, but this also is impractical for at least two reasons. First, local ranchers are unlikely to reduce cattle numbers voluntarily. Second, reducing cattle would likely boost zebra numbers, and potentially lion numbers, increasing top-down control of hartebeest. This is because the diets of cattle and zebra overlap (Kartzinel et al., 2015) and both are likely limited by rainfall (as they are in the wider Laikipia region; Georgiadis et al., 2003, 2007a) and they probably compete in dry times and places (Odadi et al., 2011). Moreover, predation by lions on cattle is rare relative to predation on because zebra (Ogada et al., 2004; O'Brien et al., 2018). Alternative conservation interventions are required for the long-term persistence of lions and their prey not only on Ol Pejeta Conservancy, but more widely in Laikipia County and the whole of sub-Saharan Africa (Bauer et al., 2015).

The extent to which our results generalize and can be extended to other locales depends on several factors: whether the affinity of zebra for glades (a behavioral response) translates to a numerical response (population increase); the length of time over which glades are attractive to zebra, and how the creation and eventual disappearance of glades gives rise to a dynamic landscape of risk to hartebeest (Kohl et al., 2018). In turn, predation for hartebeest varies across the landscape in accord with the density of glades, and the degree to which the attraction of zebra to glades changes with glade density. If increasing density of glades increases zebra and thus lion abundance, predation pressure on hartebeest could also increase. Or, if glades only attract zebra but do not result in population increase, increasing glade density could further disperse zebras across landscapes, negating the ability of glades to aggregate zebra.

We showed that spatial and temporal dynamics of predators and prey on Ol Pejeta Conservancy are consistent with apparent competition theory, and suggested a practical application for how lions and their secondary prey can coexist. Using strategic livestock management to manipulate the spatial distribution of predation pressure, we have provided a possible way to alleviate top-down control on an ungulate of conservation concern (Jackson's hartebeest) without resorting to lethal control of their most important predator (lions). Such solutions for conservation of lions in non-protected areas are needed to complement traditional funding efforts for formally-protected areas (Lindsey et al., 2018).

AUTHOR CONTRIBUTIONS

CN, SB, NG, and JG conceptualized the research problem. CN and JG designed the study and performed the analyses. BG and AK implemented lion capture and assisted with analyses. LP implemented the boma experiment. DR collected and analyzed data on abundance and resource selection of plains zebra. CN, SB, and JG wrote the manuscript, with edits and input from all authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00123/full#supplementary-material

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A Critical Review of Lion Research in South Africa: The Impact of Researcher Perspective, Research Mode, and Power Structures on Outcome Bias and Implementation Gaps

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Understanding the state of research, and its effectiveness, in a predominantly Life Sciences sphere, requires an assessment of knowledge growth dynamics, and the associated scientific and bibliometric impacts. We aim to create and evaluate, in a systematic review process, a macro-structure of the science generated in lion research in South Africa (SA) from 1990 to 2018. First, we classified the evidence architecture of lion research data extracted from the *Web of Science Core Collection*. Then, we identified prominent features that the datasets reveal in terms of authorship and ownership, as defined by first author affiliation and geographical location. Fifteen sub-disciplines were identified to characterize the topics. From 2000 onwards, multidisciplinary and interdisciplinary contributions started to emerge, catering for research problems defined at the interface of the academic-practitioner domains. These included social and economics components, and were aligned with conservation framings that seek to evaluate conservation within market-based vs. people-based approaches. Study areas were concentrated within SA (61.8%) and the remainder was either conducted in the rest of Africa (22.9%), or in various combinations of geographical focus. Author affiliation indicated that 63.1% of first authors had a South African affiliation. The rest of Africa was poorly represented at 2.4%. The majority (57.1%) of the first authors was male, but from 2014 to 2018, female researchers outnumbered males; however, male first authors continued to be cited more frequently. Furthermore, we provide a systemic analysis of the way in which research contributes to lion conservation. Overall, three voices dominate this area. Firstly, Mode 1 research has been driving research output in a "vicious circle," motivated by researchers' quest for accumulating academic rewards. Secondly, the citation impact shows a gender disparity against the recognition of female researchers. Lastly, a power imbalance against authors from the rest of Africa became apparent, whereby their role is mainly shaped toward being team contributors. This research shows that effective conservation requires appropriate knowledge to be generated, and this to be effectively translated into practical applications, while considering all perspectives in order to provide the opportunity for balanced contributions and influences. Imbalances such as the ones revealed above are likely to prevail more broadly.

Keywords: lion research, South Africa, bibliometric analysis, research mode, citation analysis

INTRODUCTION

Conservation provides an interesting discipline space in which to consider how we go about doing research, because it has evolved both in terms of the methodologies as well as the socio-political dimensions, and in how its importance is defined by society (Fazey et al., 2005; Kareiva and Marvier, 2012). In general, the approach used to conceptualize an issue significantly impacts the ways in which it is perceived and framed, and, hence, defines the types of responses, and solutions that actors involved in the process create to address it (Nisbet and Scheufele, 2009; Newell et al., 2014). This means that conceptualizations reveal both how we "know," and the future knowledge that can be shaped. Conservation has a history of plural views that continue to co-exist: starting with the seminal concept in which emphasis was placed on species/habitats/wildlife ecology (Nature for itself) which gradually shifted to ecosystems level through population biology/natural management (Nature despite itself) and, then, ecosystem functions/environmental economics (Nature for people) (Mace, 2014). These different framings guide the ways through which conservation is defined, and define the purposes it serves. Such long-held debates reverberate in the current "new vs. traditional conservation" debate (Holmes, 2015). For instance, questions have arisen as to whether poverty alleviation should form part of the undertaking of conservation (Roe, 2008) or whether true wilderness exists and its validity as a concept for conservation (Callicott and Nelson, 1998). At another level of debate, conservationists advocate for, and critique working with corporations and capitalism (Brockington and Duffy, 2010). In the new-conservation debate, the existence of two opposing positions on the motivations and means to approach conservation (Holmes, 2015) has resulted in the stifling of other relevant debates in conservation social science, such as those on biocultural diversity (Holmes et al., 2017). This indicates that there is a research-implementation gap in conservation assessment works. As far as three decades back, Soulé's (1986) landmark paper cautioned against the mission-driven discipline approach (Meine et al., 2006) in the conservation sciences, as it curbs active engagement with "real world problems, circumstances, and experiences". Consequently, even though scientific knowledge accumulates, the results are not translated into management actions. Recently, Toomey et al. (2017) reiterated that such issues have become pervasive over time. Even though the research-implementation gap approach has proposed a number of solutions to address pervasive problems in the form of evidence-based conservation, conservation evaluation, and science communication (Knight et al., 2008; Arlettaz et al., 2010; Matzek et al., 2014; Toomey et al., 2017), very little effort has been focused on whether these represent an accurate description, and actions, to address real world challenges. In the first article of this special series themed on "How Prides of Lion Researchers are Evolving to be Interdisciplinary," the analysis performed by Montgomery et al. (2018) revealed that interdisciplinarity has been historically low even within the human-lion conflict research, which is inherently a multi-dimensional component, although efforts to incorporate more inclusivity are apparent. The most recent "People and Nature" conservation framing attributes a great significance to interdisciplinary, social, and ecological sciences (Mace, 2014), hence, paving the way for a more strategic research agenda with various configurations to create knowledge and understanding for both researchers and practitioners.

This paper is embedded within the context of lion, *Panthera leo*, research in South Africa, and provides a case study for understanding the many dimensions of how we go about doing science, and who is doing the work, and, therefore, shaping the interpretation, and the outcomes of science. Lions are a charismatic and flagship species (Courchamp et al., 2018; Montgomery et al., 2018), which is iconic to the public who has an interest in the species, as reflected in the large number of documentaries that have been made on lion biology, lion conservation, and lion-human interactions (Somerville, 2017; Albert et al., 2018). Importantly, the domain represents a large enough body of work to enable us to discern patterns, including over an extended period of three decades of lion research by South African-based authors. Even on the global scale, the African lions are among the most extensively studied and protected carnivores (e.g., Packer et al., 2013), but their population is declining, and they are listed as Vulnerable on the IUCN Red-list (Bauer et al., 2016). Factors causing lion population decline include: habitat loss which has resulted in the reduction of the lion's range by 75% (Riggio et al., 2013), the intensification of human–lion conflicts because lions prey on livestock (Woodroffe and Frank, 2005; Kissui, 2008), and attack people (Packer et al., 2005a, 2011a), over-harvesting in inadequately regulated sport hunting (Packer et al., 2009, 2011b) which can extend into non-hunting National Parks (Loveridge et al., 2007; Caro, 2008; Kiffner et al., 2009), inbreeding in genetically isolated populations (Slotow and Hunter, 2009) leading to measurable reductions in reproductive rates and disease resistance in small populations (Kissui and Packer, 2004; Trinkel et al., 2008, 2011). Despite these trends, literature also shows a number of successful population restoration interventions, as seen in the Serengeti lions (Packer et al., 2005b), several large South African National Parks (Ferreira and Funston, 2010; Funston, 2011), and private reserves across sub-Saharan Africa (Hunter et al., 2007; Lindsey et al., 2009a,b; Slotow and Hunter, 2009). However, contrasting approaches have emerged with regards to the economic and social feasibility of management practices, such as fencing or kraaling of livestock (Hunter et al., 2007; Hayward and Kerley, 2009; Slotow and Hunter, 2009; Creel et al., 2013; Packer et al., 2013). The lion being an apex predator, it can have profound effects on ecosystem functioning and structure (Tambling et al., 2013). Literature shows that research activities focus on scrutinizing the lion both in single species studies (Creel et al., 2016; Henschel et al., 2016; Lindsey et al., 2016), and in relation with other predators (Cozzi et al., 2012; Vanak et al., 2013; Swanson et al., 2014), herbivores (Valeix et al., 2009; Meena et al., 2014; Martin and Owen-Smith, 2016) and relevant conservation management practices (de Pinho et al., 2014; Winterbach et al., 2014; Snyman et al., 2015). Therefore, the African lion proves to be a rich academic, applied, and socially relevant species as a focus for a bibliometric assessment such as conducted here.

The literature shows that over time, complex and real-world issues impacting lion conservation research had to be addressed in such a way to counteract problems such as: the "culture clash" between scientists and managers (Roux et al., 2006; Gibbons et al., 2008); weak interdisciplinarity capacity resulting in the inability of the scientific community to connect science with societal needs (McNie, 2007); insufficient expertise and/or literacy on the side of managers and practitioners (Sunderland et al., 2009); poor stakeholder or practitioner participation in the strategic enactment of conservation (Knight et al., 2008; Shaw et al., 2010); non-recognition of scientists' participation in policy or practice by the academic reward system (Shanley and López, 2009; Arlettaz et al., 2010); and, mismatches in scale, budget, or approach between research experiments and management efforts (Hulme, 2003; Kuebbing et al., 2013). The emergence of integrated research with social and economic components in conservation management practices, hunting, human-wildlife, tourism, is in line with the surfacing trends of, on the one hand regulatory vs. capitalist-driven approaches regarding biodiversity management—managing nature to maximize the overall value of the human condition (Dressler and Roth, 2011; Jepson and Ladle, 2011; Hugé et al., 2017), and, on the other hand, the nature protectionist vs. the more development-oriented social conservationist approach (Miller et al., 2011). The utilitarian perspective emerged as it became increasingly clear that conservation has a cost (Hugé et al., 2017). The eclectic and multiple nature of disciplines in conservation has emerged because all components of human activity (economics, business management, economic viability forecasting, trade, human-wildlife conflict, conservation tourism etc.), are ultimately linked to the state or efficiency of conservation efforts (Hutton et al., 2005; Mace, 2014; Soulé, 2014), yet approaches used to define research questions differ. As a means to enhance the concepts articulated by the dichotomous conservation framings, Holmes et al. (2017) identified three main schemes: (i) conservation to benefit people but opposing links with monetization, capitalism and corporations; (ii) bio-centric approaches, labeled as traditional conservation 2.0, and (iii) a framing representing a more instrumental view of the importance of benefiting people as a means to landscapes, also termed as the new conservation approach with an optimistic outlook on the use of market-based instruments. These are partly overlapping framings that can be used as entry points, depending on the decision-making context. These changes in research mode landscape represent attempts to respond to research-implementation challenges in the conservation sciences, including the lion as a species.

In addition to the discussion on the research mode within Nature conservation, we frame the power relations that shape lion conservation research from two different angles. In the first instance we assert that since the lion distribution range is limited to components of the global South, this makes it interesting for scrutiny from a North-South relations assessment point of view. This position on research collaboration has been under scientific scrutiny by a number of researchers in the higher education and international research partnership field (Jentsch and Pilley, 2003; Galvin and Haller, 2008; Confraria et al., 2017). The literature emphasizes the need for partnership, and its related principles, for researchers between developed countries and the rest of the world, whilst its critics highlight the problematical context of structural inequality and historical legacies which are antithetical for the development of mutually beneficial collaborations (Koch-Weser and Yankauer, 1993). More recently, Yarmoshuk et al. (2016) alluded that current systematic mappings of the basic, common characteristics of North-South research partnerships are scarce. This state of affairs, therefore, presents an open space for investigation within lion conservation research. The second aspect covers power in terms of gender representation in the research community (Bonnet et al., 2004), and, more specifically, in ecology and conservation (Martin, 2012; Pettorelli et al., 2013). Apart from enlightening the research community on the condition of the research carried out and knowledge produced, power relational issues are also of general interest to the public in order to understand the configuration of researchers who are at the forefront of lion research, and the resulting influence that their work may have. Besides the emergence of more complicated approaches, when considering application of the work to solve real-world problems posed by conservation needs, one also has to understand the foundational disciplines from which the evidence is derived for robust understanding. Not only have interest or capacity in certain disciplines changed over time (Di Marco et al., 2017), but the balance across disciplines may also be important for balanced decision-making (Martín-López et al., 2009). The "power" or "voice" of certain disciplines, or, rather, the scientists within those disciplines that may champion or influence thinking and understanding, may not be balanced.

In this paper, we use lion research based in South Africa as a case study to understand the following questions: (1) What is the approach that has been taken (alpha-science through to transdisciplinary), and how has that changed over time? (2) What are the sub-discipline areas that are researched? (3) Does the work focus on lions, or multiple species? (4) Who is leading the research (gender relations, SA based or from abroad), and in which sub-disciplines? (5) How can we assess the inclusion of social science methodologies to evaluate "people and conservation" issues, and economic approach to evaluate "capitalist conservation" issues? For each of these areas, we evaluate how this has changed over the three decades from 1990. In addition, we analyze where the work has been published, and the citation of the work as a measure of impact.

MATERIALS AND METHODS

The study is comprised of a retrospective bibliometric analysis in the *Web of Science Core Collection* on lion research conducted with at least one author with a South African affiliation. In order to capture the overall contribution of the South African-led lion research, the total number of publications covering *Panthera leo* as a topic was determined as "TS = *Panthera leo.*" The search returned 1,087 publications. Following screening for relevance, 937 publications were retained.

For the second search where emphasis was laid on lion research carried out with at least one author bearing a South African affiliation, the main search topic, "TS" was "*Panthera leo.*" This was combined with the "AND" operator to link the search term with articles that has at least one author with "South Africa" as an address affiliation. This search allowed for the accrual of 262 research articles. Following screening, 249 articles *(n = 249)* were retained for scrutiny: 13 articles were omitted from the list (one commentary and 12 articles did not constitute research aspects related to lions).

A third bibliometric search was performed in order to assess whether there is any participation of African authors outside of South Africa, having conducted lion research in South African study sites, without the co-authorship of South African researchers. The search criteria for topic was defined as TS = "*Panthera leo* AND South Africa." Additionally, the address criterion, AD, was robustly expressed as: "Ägypten OR Algeria OR Algerie OR Algerië OR Algérie OR Algerien OR Algeriet OR Algerije OR Algieria OR Angola OR Äquatorialguinea OR Argelia OR Argélia OR Äthiopien OR Benin OR Benín OR Bénin OR "Boerkina Fasso" OR "Botsuana OR Botswana" OR "Burkina Faso" OR "Burquina Faso" OR Burundi OR "Cabo Verde" OR Cameroon OR Cameroun OR Camerún OR "Cape Verde" OR "Cap-Vert" OR "Centraal-Afrikaanse Republiek" OR "Central African Republic" OR "Centralafrikanska republiken" OR Chad OR Chade OR Comoras OR Comore OR Comoren OR Comores OR Comoros OR Congo OR "Costa do Marfim" OR "Côte d'Ivoire" OR "Cote d'Ivoire" OR "Côte d'Ivoire" OR Czad OR Djiboeti OR Djibouti OR Djibuti OR Dschibuti OR Dzibuti OR Egipt OR Egipte OR Egipto OR Egito OR Egypt OR Egypte OR Égypte OR Egypten OR Ekvatorialguinea OR "Ekvatorial-Guinea" OR "Ekwatoriaal-Guinee" OR Elfenbenskusten OR Elfenbenskysten OR "Equatoriaal-Guinea" OR "Equatorial Guinea" OR Eritrea OR Eritreia OR Érythrée OR Erytrea OR Ethiopia OR Ethiopië OR Éthiopie OR Etiopia OR Etiopía OR Etiópia OR Etiopien OR Gabão OR Gaboen OR Gabon OR Gabón OR Gabun OR Gambia OR Gâmbia OR Gambie OR Gambië OR Gana OR Ghana OR Guiné OR "Guiné Bissau" OR "Guiné Equatorial" OR Guinea OR "Guinea Bissau" OR "Guinea Ecuatorial" OR "Guinea-Bissau" OR Guinee OR Guinée OR "Guinée équatoriale" OR "Guinee-Bissau" OR "Guinée-Bissau" OR Gwinea OR "Gwinea Bissau" OR "Gwinea Równikowa" OR Ivoorkus OR Ivoorkust OR "Kaap Verde" OR Kaapverdië OR Kameroen OR Kamerun OR "Kap Verde" OR "Kapp Verde" OR Kenia OR Kenya OR Komoren OR Komorene OR Komorerna OR Komory OR Konga OR Kongo OR Kongo OR Lesotho OR Lesoto OR Liberia OR Libéria OR Liberië OR Libia OR Líbia OR Libië OR Libya OR Libye OR Libyen OR Madagascar OR Madagaskar OR Majotta OR Malawi OR Maroko OR Marrocos OR Marruecos OR Mauretania OR Mauretanien OR Maurice OR Mauricio OR Maurício OR Mauritania OR Mauritânia OR Mauritanie OR Mauritanië OR Mauritius OR Mayotte OR Moçambique OR Morocco OR Mosambiek OR Mosambik OR Mouritanië OR Mozambik OR Mozambique OR Namibia OR Namíbia OR Namibie OR Namibië OR Niger OR Níger OR Nigeria OR Nigéria OR Nigerië OR Oeganda OR Ouganda OR Principe OR Quênia OR "República Centroafricana" OR "República Centro-Africana" OR "República dos Camarões" OR "Republika Południowej Afryki" OR "Republika Srodkowoafrykanska" OR "Republika Zielonego Przyladka" OR "République Centrafricaine" OR Reunião OR Reunion OR Reunión OR Réunion OR Ruanda OR Rwanda OR "Saara Ocidental" OR "Sahara Occidental" OR "Sahara Zachodnia" OR Sambia OR "Santo Tomé" OR "Sao Tome" OR Senegal OR Sénégal OR "Sentraal-Afrikaanse Republiek" OR "Sentralafrikanske republikk" OR "Serra Leoa" OR Seszele OR Seychelle OR Seychellen OR Seychellene OR Seychellerna OR Seychelles OR "Sierra Leona" OR "Sierra Leone" OR Simbabwe OR Soedan OR Somalia OR Somália OR Somalie OR Somalië OR "Sør-Sudan" OR "Soudan du Sud" OR "South Sudan" OR Suazi OR Suazilandia OR Suazilândia OR Sudán OR Sudão OR Südsudan OR "Suid-Soedan" OR Swasiland OR Swaziland OR Sydsudan OR Tansania OR Tanzania OR Tanzânia OR Tanzanie OR Tanzanië OR Tchad OR Togo OR Tschad OR Tsjaad OR Tsjad OR Tunesië OR Tunesien OR Túnez OR Tunezja OR Tunisia OR Tunísia OR Tunisie OR Tunisië OR Tunisien OR Uganda OR Västsahara OR "Vest-Sahara" OR "Wes-Sahara" OR "Westelijke Sahara" OR "Western Sahara" OR "Westsahara" OR Zambia OR Zâmbia OR Zambie OR Zambië OR "Zentralafrikanische Republik" OR Zimbábue OR Zimbabwe" in order to represent the 53 countries of the African continent (United Nations Economic Commission for Africa, 2018), except South Africa. This search returned 31 papers. Two papers were omitted due to irrelevance whereby the lion was mentioned only for referencing purposes in the Discussion section of the respective journals. Upon screening, only eight papers had a first author from a "Rest of Africa" affiliation: one from Benin, one from Kenya, and six from Zimbabwe.

Original articles were defined as reports that investigated a clearly defined study objective or hypothesis. All other types of articles were excluded from the analysis, including book reviews, case reports, commentaries, and editorials. The database included the following indexes: SCI-EXPANDED, SSCI, A&HC1, ESCI.

A number of article characteristics, which are broadly characterized into two categories, were assigned to each article. In the first category, metrics-based screenings that were derived directly from *Web of Science* database include: (i) number of citations per articles, (ii) whether the article was published in a South African or international journal, and (iii) countries listed in the author affiliation. In the second category, we extracted 10 article characteristics for each article from the abstract, or, if not clear, from reading the full article: (i) mode of disciplinarity, (ii) justification for degree of disciplinarity (see **Supplementary Material**), (iii) single species or multiple species studies, (iv) the countries of study site(s), (v) the science disciplines covered, (vii) the inclusion of social-science and/or economics component to the research, and accompanying justifications, (viii) classification of the journal type based on its degree of disciplinarity, (ix) classification of the main thematic discipline associated with the journal, (x) gender of the first author. All study authors were classified as either male or female according to the first or middle name listed in the article, with the understanding that many names are associated with only one gender (e.g., "Mary" is female and "Henry" is male). If only initials of the first name were used in the list of authors, we sought further publications from the same group of authors or performed an Internet search using the Google search engine to find the first name. If an author's gender could not be ascertained by initial inspection of his or her first name alone, attempts were made to locate gender-specific information about that author by performing Internet searches, and by visiting personal or institutional websites (in several instances, the sites included photographs or curricula vitae). Authors of two papers were excluded because their gender could not be determined even by these additional means.

Expert opinion, of the second collaborator, Rob Slotow, was used to group each journal article according to the five modes of research, namely: α-science, disciplinary, multidisciplinary, interdisciplinary, and transdisciplinary. Insights were drawn from a conceptual framework (**Supplementary Material**) to distinguish among the modes of research applied in each paper. As a means to obtain clarity on the ways that research sub-components self-organize with increasing complexity in the multidisciplinary and interdisciplinary modes, systems approach diagramming techniques, in the form of (i) influence and (ii) Ishikawa fishbone diagrams (Kudryavtsev and Gavrilova, 2017) were applied to observe the aggregation of sub-components around higher level concepts. Furthermore, we apply a cause-and-effect analysis from a systems thinking perspective (Reynolds and Holwell, 2010) and systems dynamics concepts (Morecroft, 2015) in order to (i) structure the interplay of linkages that govern the ways in which research has been conducted in lion conservation, and, (ii) identify whether there is a shift, if any, which is gaining momentum in shaping current conservation understanding.

The country affiliation of each first author was categorized as USA, Europe, South Africa, rest of Africa, or other countries (Other). Using the InCites™ tool of Web of Science/Thomson Reuters (WoS™), we applied bibliometric and author profiling to evaluate which countries in the world are producing research with higher research citation impact. Presently, there are several measures to calculate citation impact indicators. From basic calculations such as: raw citation counts; citations per publication; the h-index; geometric means (Fairclough and Thelwall, 2015) to field normalized citation score (Waltman et al., 2011), source normalized indicators (Waltman and van Eck, 2015), amongst others. For the purposes of this study, raw citation counts, and citations per publications, were used. For the citation pattern analysis, we divided papers into three periods: those published in 1990–2005, in 2006–2013, and from 2014 to 31 August 2018. The division into three periods took into account: creating a time series which allowed us to understand change in pattern over time; the number of papers published over time; getting a reasonably balanced sampling; providing fairness for papers to accumulate citations; and being comparable within a time period. This resulted in unequal duration of time periods, but ones which we believe provide insights without inordinate bias in any particular direction. The time periods were decided *a priori*, and then the analysis of patterns undertaken, so that there was no bias of the results influencing the time periods selected. Furthermore, we applied Wagner et al. (2011) structuralist lens, that subsumes both cognitive (knowledge disciplines, citations) and social structures, i.e., power relations in lion research in terms of research ownership and first authorship gender representation.

RESULTS

The general search conducted on the "*Panthera leo*" topic generated 937 research papers published from 1990 to 2018 in the *Web of Science Core Collection* database. In the second and more focused bibliometric search, we returned 249 unique lion research papers with at least an author having a South African affiliation. This represents 26.6% of the total number of publications based on the "*Panthera leo*" topic (**Table 1**). **Table 1** shows the distribution of papers by geographical location of study area and first author affiliation. The majority of the studies were conducted in South Africa (61.8%), followed by the "Rest of Africa" locations (22.9%). It is noteworthy that despite the geographical range of the lion and its importance for conservation understanding and management, only 22 studies (8.8%) out of the 249 shared South Africa and the "Rest of Africa" as study sites. In contrast, with respect to the first author affiliation of the papers, South African, European and USA affiliations share the majority of representation at 63.1, 17.3, and 14.5%, respectively. Only 2.4% of the papers of the "Rest of Africa" countries have a first author affiliation. For the third bibliometric search where the focus was on identifying whether "Rest of Africa" authors have been leading (as first authors) lion-related research in South Africa, the dataset constituted of 31 publications. Only eight of these publications bear first authors from the "Rest of Africa" and none of these eight publications involved South Africa as part of their study site. This indicates that "Rest of Africa" authors have not been leading any lion-related research by using South Africa as part of their study site(s). Moreover, five of these papers included co-authors from first world countries, that is, Europe and USA.

Of the 249 papers, 50 papers (20.1%) were published in a South African journal. 221 (88.8%) papers were published in journals which were categorized as having disciplinary audiences. The rest appeared in journals with a multi-disciplinary focus. In terms of research mode, α-science

TABLE 1 | Distribution of papers by geographical location of study area and first author affiliation.

Geographical location		First author affiliation	
Study area	**Papers published**	**Geographical region**	**Papers published**
South Africa	154 (61.8)	South Africa	157 (63.1)
Rest of Africa	57 (22.9)	Europe	43 (17.3)
SA + Rest of African countries	22 (8.8)	USA	36 (14.5)
SA+ Rest of Africa + Other countries	10 (4.0)	Rest of Africa	6 (2.4)
SA + Other countries	3 (1.2)	Other countries	7 (2.8)
Europe	2 (0.8)		
SA+ Africa +Europe	1 (0.4)		
Total number of papers on the topic *Panthera leo*			937
Number of these papers with a South African body as affiliation			249 (26.6)

Figures in brackets indicate percentage. SA, South Africa.

comprised 10.8% of papers, disciplinary 59.8%, multidisciplinary 17.7%, interdisciplinary 11.2%, and transdisciplinary 0.4% of the papers (**Figure 1A**). Following the systematic scrutiny of the 249 journal articles, 15 sub-disciplines were identified as forming the researched components in lion research (see **Figure 1B**). The majority of papers were veterinary science-based, studied lion predation and their prey, or lion population studies, or addressed conservation issues. Research at the α-science level was more focused on increasing the mechanistic understanding of the life science aspects in lion research, from veterinary sciences, physiology, population, predation, or paleobiology studies. At the disciplinary and multidisciplinary level, the research foci were more widespread across all the research sub-disciplines. In contrast, interdisciplinary research constituted mostly of the investigations within the conservation, hunting, human-wildlife conflict, and tourism domains. There was a marked increase in studies in the multidisciplinary and interdisciplinary mode over time (**Figure 1A**). Only one article of the 249 which studied conservation and cross-border trade of bones, was classified as transdisciplinary (**Figure 1B**).

Multiple species research was mostly conducted within disciplinary studies (38.2%), and multi-species study was not a requirement for multidisciplinary or interdisciplinary work (**Figure 1C**). 111 articles researched the lion as the single species under investigation. Multispecies papers included other intraguild predators, mostly multiple species (44.6%), cheetah *Acinonyx jubatus* (4.0%), hyaenids (2.4%), wild dogs *Lycaon pictus* (2.0%), or leopards *Panthera pardus* (1.6%). Ungulates were studied mainly with respect to their role in the prey-predator dynamics and human-wildlife conflict. Pathogens such as parasites, bacteria, and viruses of lion or other carnivores comprised 18 (7.2%) papers.

The contents of multidisciplinary papers were mapped out in order to observe how the different components aggregate into knowledge clusters using an influence diagram (**Figure 2A**), and three main clusters were identified: genetics and disease, biology and conservation, and socio-economic factors (**Figure 2A**).

20 articles (8.0%) used social science methods and/or economic analyses, and, interestingly, these were published mainly in disciplinary ($n = 14$), rather than multidisciplinary ($n = 1$), or interdisciplinary ($n = 5$) journals. Only a single article was categorized as transdisciplinary. It dealt with transborder bone trade, and was published in a multidisciplinary journal. We use a fishbone diagram, which is primarily used for problem identification in complex situations, to portray the social and economic components within the lion research database. Each branch represents a major research theme, and the associated sub-themes correspond to specific research problems addressed in that paper. The upper portion of the diagram illustrates five main research components for social and practical management (**Figure 2B**). Hunting and conservation dealt with the surveys of hunting, the co-production of reward system among stakeholders, and appraisal of hunters' skill in age estimation of lions. Researchers also engaged with communities to assess the impacts of kraaling and herding. A number of studies assessed the ways and means to improve conservation through survey methodology carried out by practitioners. The social implications of human-wildlife conflict were assessed in order to determine the tolerance level of communities under conflictual situations. Interviews and focus group discussions were carried out to identify reform needs, and to facilitate the changing of community behavior on herding practices, and identify their education needs in this respect.

The lower portion illustrates the economic implications of conservation (**Figure 2B**). One research paper, classified as TD, quantified cross-border bone trade. The economics of hunting and conservation involved studies to understand the economic off-take involved in hunting, and surveys of hunting sales, operations, and clients, and also an assessment of the cost of conservation, and an evaluation of extra-limital species and the associated conservation risks. Prediction and modeling techniques were applied in the development of business management models for conservation tourism-based activities, and used to identify the potential for optimizing income from hunting. Conservation management practices such as kraaling and herding were evaluated for their economic feasibility. Predator management studies focused on the biology and economics of reserves. The impacts of predation on the economic sustainability of the communities were also investigated. As part of creating understanding on the economic implications of human-wildlife conflict, expert surveys were conducted to gather information on the ways to maximize investment in conservation against risks from socio-economic factors. Studies also assessed the value of different types of land use, and the threat of diseases.

The number of citations accumulated by research modes over time provides an idea of the knowledge base being used to scrutinize the lion in wildlife conservation research. The disciplinary mode remained pervasive (59.8%), with the highest proportion of citations over time, compared to α-science (10.8%), multidisciplinary (17.3%), or interdisciplinary (11.2%) works. Transdisciplinary research in lion research

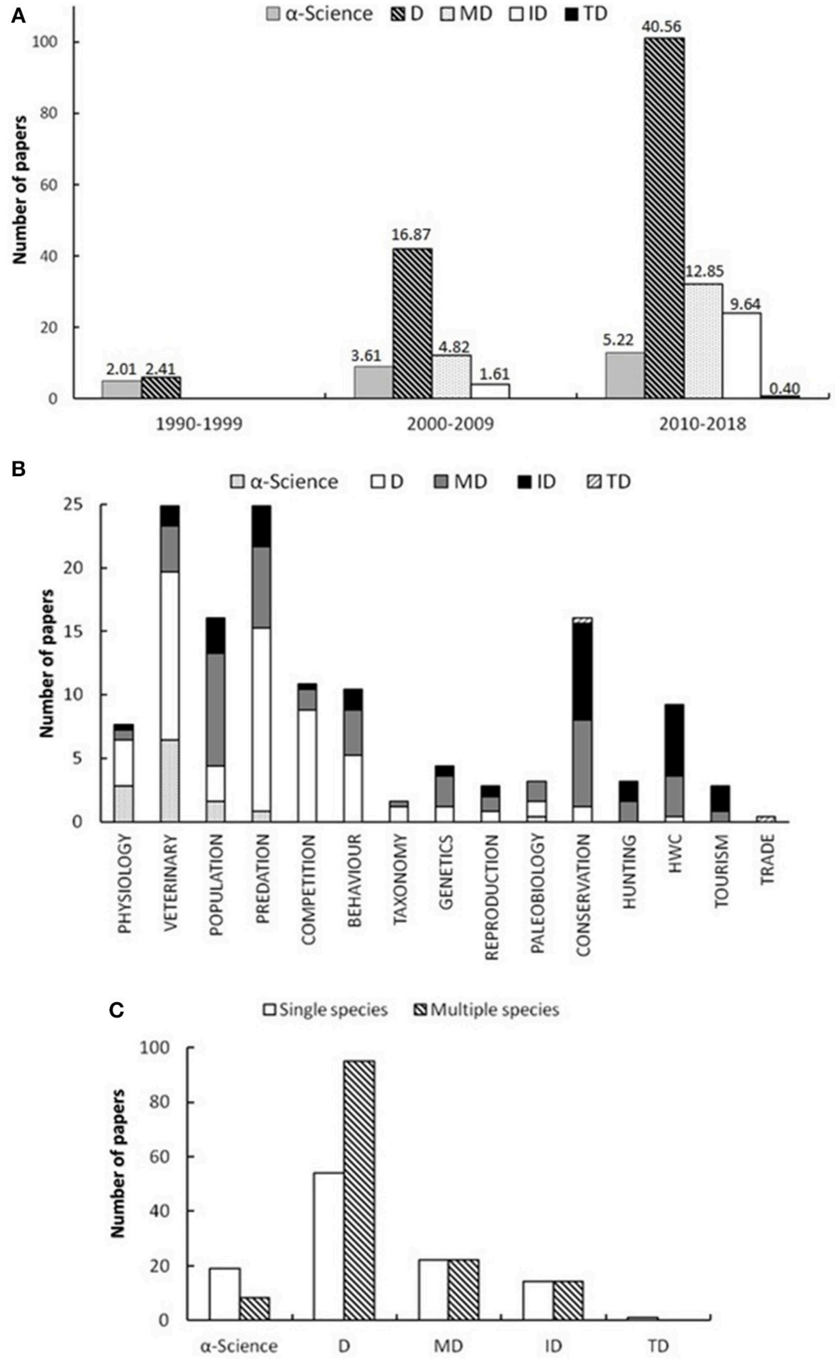

FIGURE 1 | Patterns of publication of papers on lions with South African authorship. **(A)** Evolution of mode of research over time (D, Disciplinary; MD, Multidisciplinary; ID, Interdisciplinary; TD, Transdisciplinary). Number indicates percentage in that category of 249 papers. **(B)** Classification of research components (sub-disciplines) studied in the research articles, noting that an article may have included more than one component, categorized by mode of research as per **(A)** (HWC, Human-wildlife conflict). **(C)** Single species vs. Multiple species as focus of study, grouped by mode of research.

is new and has the lowest percentage of citation at 0.8%. Compared to 1990–2005, the period 2006–2013 shows the recognition of more collaborative works at the multidisciplinary and interdisciplinary levels (**Figure 3**). For the first decade, there was a single citation for an ID paper, whereas in the second and third decades, ID papers accumulated 14 and 13 citations, respectively. This represents an interesting trend. Even though the number of papers that fall into the multidisciplinary and interdisciplinary modes were small in the pre-2006 period, their impact was high since the number of

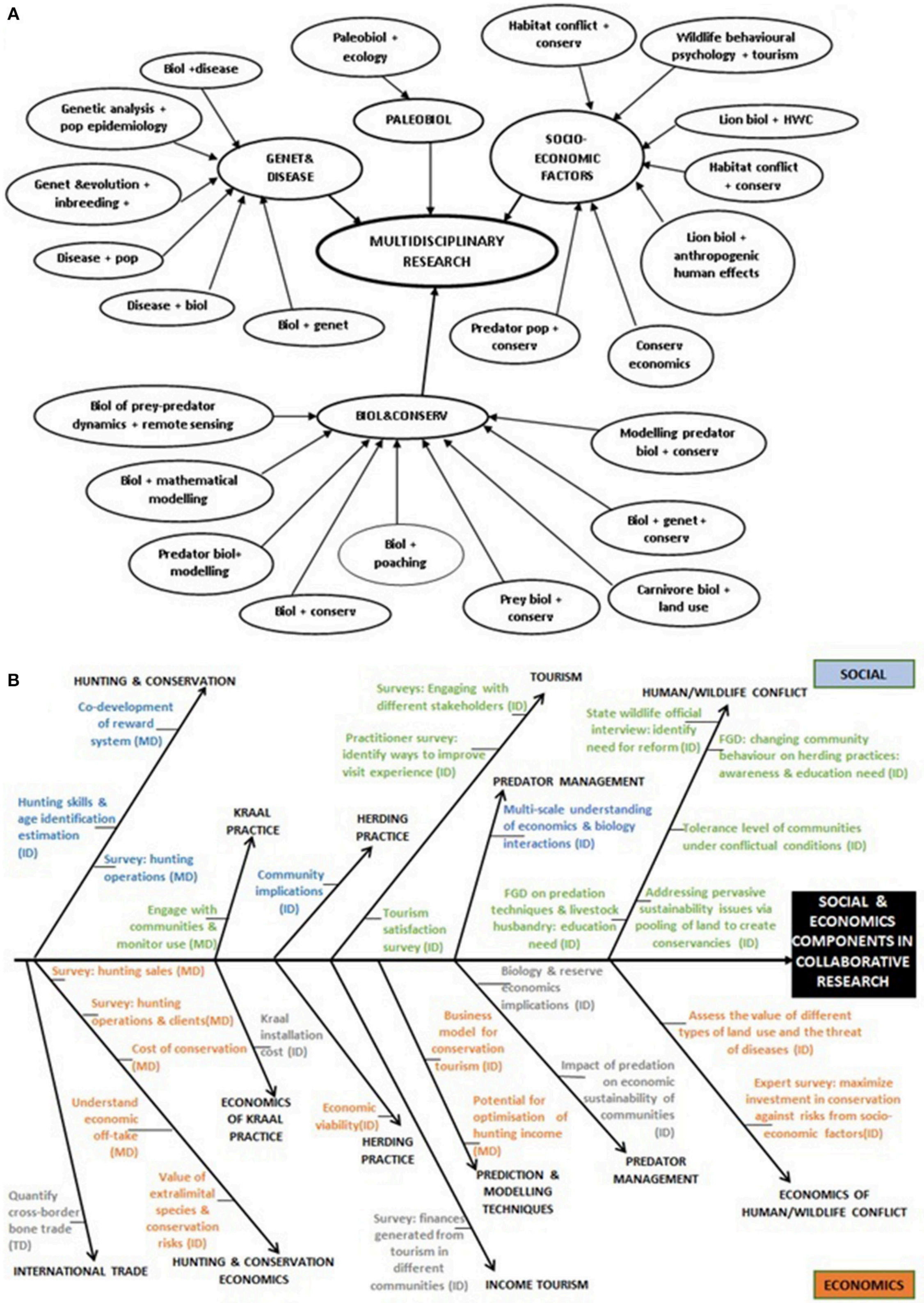

FIGURE 2 | Components of multidisciplinary and interdisciplinary research. **(A)** An influence diagram representing the research components of Disciplinary work. Biol, biology; Conserv, conservation; Genet, genetics; Paleobiol, paleobiology. **(B)** A fishbone diagram contrasting the work that included a social and/or economic component to it. The mode of research is indicated in brackets. FGD, Focus group discussions.

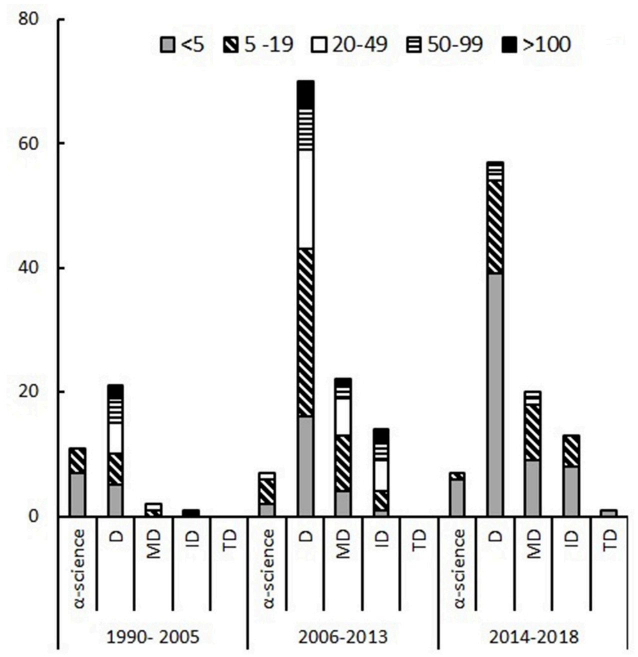

FIGURE 3 | Evolution of journal citations for papers published in different modes (n = number of citations in each category).

citations earned were up to 49 for MD papers and >100 for the ID papers. Overall, citations for alpha-science remained comparatively low compared to papers in the discipline research mode. No α -science studies were cited more than 50 times (**Figure 3**). For the most recent time frame, no paper has reached >100 citations due to the time lag required to accumulate citations.

In terms of citations cumulated by single and multiple species papers, the general trend was that both single species and multiple species papers fluctuated over time with a marked increase from the year 2000 onwards. However, researchers cited multi-species papers more frequently than those where the lion was investigated as a single species, especially after 2005 (**Figure 4**). For multiple species papers, citations peaked at $n = 557$ for the year 2008 whereas for papers published where the lion is observed as a single species, the citation number peaked at $n = 360$ for the year 2013.

For all three periods, the majority of the papers were from a South African first author affiliation, but this decreased from 69 to 57% and then 60% over time (**Table 2**). Interestingly, in 1990–2005, Europeans were first authors for about 30% of the papers, but in 2006–2013, this dropped to 22% while 15% of papers were from USA first authors. In 2013–2018, the European first authors dropped to 14%, and USA first authors increased to 22%. Overall, there have been few papers with first authors from other African countries that included an author with a South African affiliation. In terms of gender of the South African first authors, in 1999–2005, 35% of them were female; in 2006–2014 they dropped to female ratio of 23%; and this has now increased to 44% female in 2013–2018 (**Table 2**). The international authors were predominantly female, but this shifted over time such that they became 56% male (**Table 2**). The works of South African first authors are the most cited across all categories (**Table 2**). Despite the charismatic nature of lions, and the important conservation context, 30.6% of the papers published in 1990–2005, and 20.4% of papers in 2006–2013 were cited <5 times, indicating little impact of a large component of the work. By contrast, 20.3 and 16.8% of the papers from 1990–2005 to 2006–2013 were cited >50 times, indicating a relatively high impact of the work. The papers led by "Rest of Africa" authors were poorly cited (**Table 2**).

Moreover, the third bibliometric search returned 31 papers and upon screening, only eight papers had a first author from a "Rest of Africa" affiliation: one from Benin, one from Kenya, and six from Zimbabwe. The main implication of this result is that none of these eight publications involved South Africa as part of their study site(s), indicating that "Rest of Africa" authors have not been leading any lion-related research by using South Africa as part of their study site. Moreover, five of these papers included co-authors from first world countries, Europe and USA.

Table 2 Distribution of citations for first authors by affiliation country and gender between 1990 and 2018, divided in three periods (n = number of papers in each category, the percentage for each decadal category are given in brackets). The grand total for the citations in the "1990–2005" period amount to 36 instead of 38, since two entries for South Africa were omitted for lack of reliable gender classification. The sub-totals and grand total represent the number of papers in each sub-category and overall distribution sum.

Generally, male researchers have earned more citations than their female counterparts, and from 1990 to 2018, female researchers (first authors) have never been cited >100 times (**Table 2**). Following compilation of gender representation and the removal of multiple entries for each author, the gender proportion of researchers in the lion research community consisted of 57.1% ($n = 89$ authors) different male and 42.9% female ($n = 67$) authors. Interestingly, the trends in the last 4 years also indicate that there are currently more papers with female than male authors.

In light of the above analysis, we created a conceptual diagram of the framing and contextualization of research on lions by South Africa-affiliated authors (**Figure 5**). We used the modes of disciplinarity in the present decade (2010–2018) (**Figure 1A**), whereby all modes of research are represented, in order to illustrate research configurations in the simple-complicated-complex continuum. The thickness of the black arrows are drawn in proportion to the percentage of papers falling under the corresponding research modes, and we conclude that a vicious, rather than virtuous, cycle is in place (**Figure 5**), as the research was predominantly disciplinary or multidisciplinary, more aligned toward researcher perspective than conservation assessment, and did not link through to translation. Consequently, the types of conservation framings and biodiversity representations used in research might not fully address the complex conservation problems, but mostly serve toward academic rewards in the form of scholarly publications,

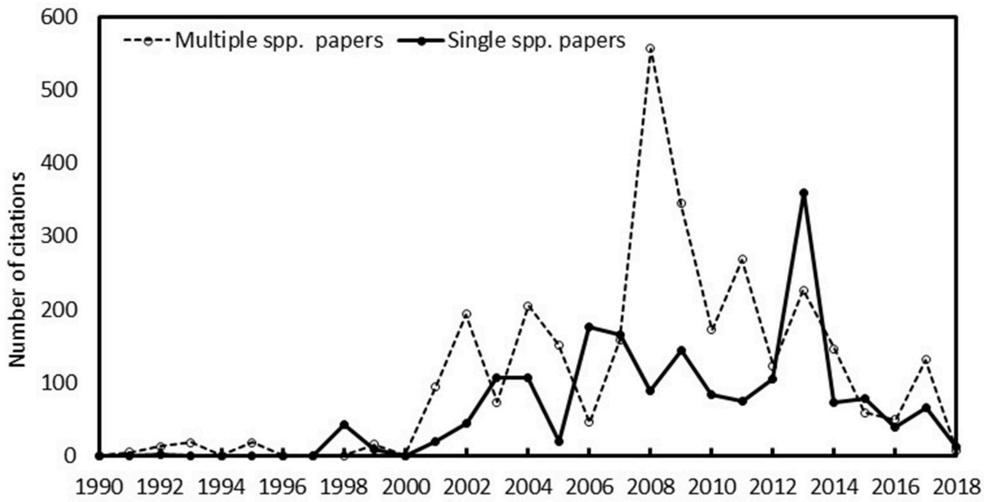

FIGURE 4 | Distribution of citations by papers with either single species or multiple species as focus of study.

and increasing the breadth of knowledge, rather than toward conservation understanding that can address needs and gaps in translation for application.

DISCUSSION

Lion research was used as a case for establishing a macro-structure of the domain, because it is a well-researched area, and is important in terms of knowledge, as well as posing challenging practical problems that need to be solved based on evidence. The lion has been subjected to much scrutiny, both as a single species and as part of multiple species investigations, to gain an understanding of this large carnivore as well as with respect to its intraguild predators and prey. Additionally, different levels of collaborative configurations make up the disciplinarity spectrum, and, over time, there has been an explosion of research.

The use of bibliometric indicators provides an opportunity to assess the pattern and impact of scientific publications, and to reveal opinionated choices by carrying out international comparisons without being invasive (Moed, 2005). A limitation of this approach is that bibliometric assessment of research performance is based on the central assumption that scientists, who have to communicate research findings, do so by publishing their findings in international peer-reviewed journals. According to Van Raan (2004), this choice unavoidably introduces a limited view of a complex reality for it might be that regionally focused papers in the Global South may contribute significantly to the local context, yet remain uncited, as researchers elsewhere are indifferent to those topics. Moreover, researchers in some countries, especially in the Global South, have different levels of access to some journal database because of financial constraints, selectivity, or publication policies (Lawrence, 2003), and, therefore, might not access journals which could have been relevant to their peer-reviewed work. Nevertheless, the aim of the current research was to establish an architecture of the state of lion conservation research based on an analysis of a leading bibliometric database.

Bibliometric data are organized in such a way that one can derive information to increase the breadth of first order learning and interpretation on a topic of interest. It was, therefore, possible to create structural relationships that provide clarity about the state of lion research by coining different benchmarks of interest. Moreover, citation analysis was also used to assess scientific impact. According to the seminal work of Merton (1973), when a given article is cited by a researcher, this is an indication that the article was somehow relevant to their study. The citing author highlights the usefulness or applicability of the information included in an article. This acknowledges intellectual or cognitive influence (Confraria et al., 2017), such that, when comparable articles are cited more times than others, the comparison translates into a measure of international scientific influence or impact (Moed, 2005), and enables international comparisons to be more objective (Garfield, 1979). A crucial aspect for analyzing the research performance of countries/regions undertaking lion-centered research is to understand whether their scientific output is having an international impact or influence. The impact of published articles can be regarded as being one crucial aspect of scientific quality, and is thus a "proxy" for quality (Moed, 2005). With increasing demands for accountability (Paasi, 2005; Steneck, 2006), the impact of research on conservation outcomes is a topic of increasing interest and importance. In the case of lion research specifically, conservation efforts often span across sub-disciplines with different knowledge bases and even across national borders. Together with Mode 1 research, which is carried out at the disciplinary level, the more complex forms of research (multidisciplinary, interdisciplinary, and even transdisciplinary) become crucial to enable a systemic expansion of the knowledge-base of research that can also inform, direct, co-facilitate translation and implementation of conservation actions.

We were able to identify epistemic variations, i.e., how do we "know," and therefore research methodology approaches, that

TABLE 2 | Distribution of citations for first authors by affiliation country and gender between 1990 and 2018 (*n* = number of citations in each category, the percentage for each decadal category are given in brackets).

Citation categories	South Africa		USA		Europe		Rest of Africa		Other		Total
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
1990–2005											
<5	7(19.4)	4 (11.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	11 (30.6)
5–19	6 (16.7)	4 (11.1)	0 (0.0)	0 (0.0)	1 (2.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	11 (30.6)
20–49	3 (8.3)	0 (0.0)	0 (0.0)	1 (2.8)	1 (2.8)	1 (2.8)	0 (0.0)	0 (0.0)	0 (0.0)	1(2.8)	6 (16.7)
50–99	3 (8.3)	1 (2.8)	0 (0.0)	0(0.0)	1 (2.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	5 (13.9)
>100	3(8.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3 (8.3)
Total	22 (61.1)	9 (25.0)	0 (0.0)	1 (2.8)	3 (8.3)	1 (2.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	36 (100.0)
2006–2013											
<5	9 (8.0)	4 (3.5)	1 (0.9)	3 (2.7)	1 (0.9)	3 (2.7)	1 (0.9)	0 (0.0)	1 (0.9)	0 (0.0)	23 (20.4)
5–19	21 (18.6)	5 (4.4)	2 (1.8)	1 (0.9)	4 (3.5)	7 (6.2)	0 (0.0)	3 (2.7)	0 (0.0)	0 (0.0)	43 (38.1)
20–49	12 (10.6)	4 (3.5)	7 (6.2)	1 (0.9)	1 (0.9)	2 (1.8)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.9)	28 (24.8)
50–99	6 (5.3)	1 (0.9)	0 (0.0)	0 (0.0)	3 (2.7)	2 (1.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	12 (10.6)
>100	3 (2.7)	0 (0.0)	2 (1.8)	0 (0.0)	2 (1.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	7 (6.2)
Total	51 (45.1)	14 (12.4)	12 (10.6)	5 (4.4)	11 (9.7)	14 (12.4)	1 (0.9)	3 (2.7)	1 (0.9)	1 (0.9)	113 (100.0)
2014–2018											
<5	24 (24.5)	17 (17.3)	4 (4.1)	4 (4.1)	6 (6.1)	3 (3.1)	0 (0.0)	2 (2.0)	0 (0.0)	5 (5.1)	65 (66.3)
5–19	8 (8.2)	8 (8.2)	6 (6.1)	2 (2.0)	2 (2.0)	2 (2.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	28 (28.6)
20–49	0 (0.0)	1 (1.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (1.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2 (2.0)
50–99	1 (1.0)	0 (0.0)	1 (1.0)	1 (1.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3 (3.1)
>100	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	33 (33.7)	26 (26.5)	11 (11.2)	7 (7.1)	8 (8.2)	6 (6.1)	0 (0.0)	2 (2.0)	0 (0.0)	5 (5.1)	98 (100.0)

The grand total for the citations for the 1990–2005 period amount to 36 instead of 38, since two entries for South Africa were omitted for lack of reliable gender classification. The sub-totals and grand total represent the number of papers in each sub-category and overall distribution sum.

characterize mechanistic knowledge (Mode 1 research–Karlqvist, 1999) vs. holistic and value-laden understanding (Mode 2–Gibbons et al., 1994) (see **Figure 5**). For instance, current findings indicate that there are a high proportion of papers which framed their research in the disciplinary mode, within which the veterinary sciences, predation, and competition and behavior components stand out, leading to Mode 1 outcomes, and feeding in a vicious cycle back to the academics and not feeding into practice. Notably, multidisciplinary and interdisciplinary work increased nearly 3-fold and 6-fold, respectively, in the second and third decades, increasing Mode 2 outputs, conservation understanding, and ability to follow the virtuous cycle of translation into practice and stimulating further problem-solving research. At the multidisciplinary level, clusters emerged, identifying the nature and reach of the scientific output in the areas of genetics and disease, biology and conservation, and social and economic components. At the interdisciplinary level, the shift in the mode of research design and the types of methodologies applied to address research questions highlight the social and economic implications of conservation assessment. Such findings suggest that the different modes of science are driving knowledge production toward the creation of systemic understanding of the conservation needs and priorities, which are aligned with the different conservation framings that would be applicable for lion research, both in South Africa and its larger geographical range. Such perspectives emphasize inextricable links among human, non-human, and ecosystem elements. For instance, at the global scale, conservation assessments have been shown to lack effectiveness in informing the delivery of conservation action (Mace et al., 2000; Whitten et al., 2001; Brummitt and Lughadha, 2003). Many of the ways in which hunting and wildlife trade operate, as well as their links to livelihood or ecosystem function, are either poorly understood or not properly taken into account (Funston, 2008; Loveridge et al., 2009; Lindsey et al., 2012). Researchers are increasingly solicited to integrate their activities with societal actors, policy-, and decision-makers into their research projects, thus creating a newly emerging model of engaged knowledge translation (Taylor et al., 2015; Western et al., 2015; Lindsey et al., 2016). Such a virtuous cycle, feeding through practitioners into practice, may be emerging in South African-authored lion research (**Figure 5**).

We use the term "biodiversity representations," here denoted by the research outcomes generated by the 15 subdisciplines, to define the types and/or combination of actors who address the research situation. We concur that this gives rise to an array of research modes resulting in the production knowledge and

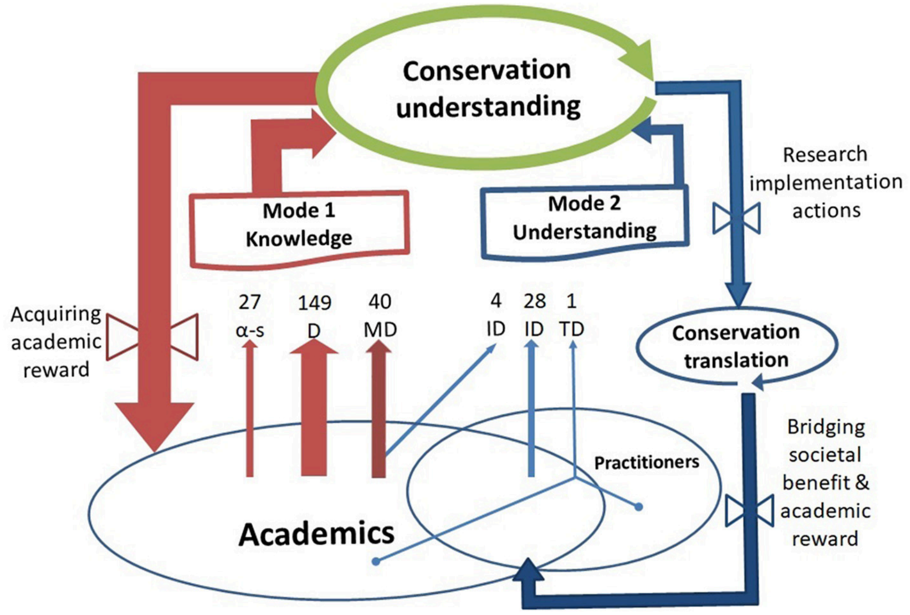

FIGURE 5 | Conceptual Framework for lion research with South African-based author for impact on society vs. purely academic outputs. For papers between 2010 and 2018, we contrast the potential actors (academic; practitioner), modes of research [α-s: α-science; disciplinary (D); multidisciplinary (MD); interdisciplinary (ID); and transdisciplinary TD], which feed into outputs classified either as Mode 1 (research focused), or Mode 2 (with some conservation assessment). This forms the knowledge base. We then connect these to conservation understanding which is made up from the different framings (Hugé et al., 2017). This then either feeds back to the actors through (i) the academics as a vicious cycle (red) which is influenced by the motivation to build academic reward only, or (ii) is translated into practice, which is regulated by research-implementation and bridging societal benefits and academic rewards actions, feeding back to the intersection of academics and practitioners as a virtuous cycle (blue). The number of papers indicates that there is currently a strong vicious, rather than virtuous, cycle in place. The thickness of the arrows representing each mode of research is proportional to the number of papers published. The interaction arrows with a valve denote systemic actions and their thickness is relative to the total number of papers they correspond.

understanding that create impact with triple-fold and perpetual cascading benefits for lion-related works. Firstly, in terms of the relevance of the impact created by research output to address complex conservation problems (Jenkins et al., 2012) and secondly, proper conservation research design ensures accountability since the study of biodiversity representations (defined by the sub-discipline categories and therefore, the research mode) involves the use of resources, there is a cost (Myers et al., 2000; Naidoo et al., 2008; Brockington et al., 2012), both real and in terms of opportunity, associated with their use as relevant indicators in prioritizing conservation research. Finally, the advantage also purports to the quality of scholarly papers published which will enrich the peer-reviewed scientific literature, and also improve the reach of practitioners in adopting scholarly publications as a means of information that drive their actions. This occurs optimally at the academic-practitioner interface (Arlettaz et al., 2010; Braunisch et al., 2012). The idea put forward here aligns with the dialectic that, on the one hand, researchers should shift from selfish self-actualizations, based solely on generating papers to gain academic rewards (Henry, 2013), to include social upliftment as part of their achievement (Fleishman et al., 2011; Cook et al., 2013), which we infer is also a means of engaging with issues of power relations by promoting inclusivity. On the other hand, practitioners should rise above the *status quo* and embrace transformative change by effectively contributing in the research process to address the research-implementation gap (Knight et al., 2008; Braunisch et al., 2012). Scientists and/or practitioners define the research by embedding the reality for the decision-making context and research design (what scale of research is required to address the problem), for a particular problematized situation (designing for problem-context specificity), based on the chosen conservation framing, which then defines the biodiversity representations (Mace, 2014; Hugé et al., 2017) to be investigated. In the present case, it is the lion and the indicators used for its conservation assessment. Ideally, starting from a consultative process between academics and practitioners, research design should be operationalized such that the "research-focused Mode 1" and "conservation assessment Mode 2" nodes interact in a self-reinforcing loop. This step would build optimum critical mass in terms of knowledge-base, conservation understanding, scale of complexity, and consensus among researchers, practitioners and other stakeholders, if applicable, to design and structure the research agendas with a pathway to translation and into practice. This creates a virtuous circle of designing and implementing research to create impact in a path-dependent and coherent way (**Figure 5**). Based on our results, we believe that lion research by South African based authors is shifting from the vicious to the virtuous circle.

Following the analysis on the modes of knowledge that constitute the lion research architecture, we scrutinized the ownership of the research. Within post-colonial discourses, issues have been raised, such as where outputs are published as well as who is identified for holding tenure of the research (Knobel et al., 2013). The question that arises in the context of this paper is to what extent is lion research in South Africa being driven by South Africans. The word "by" has been carefully used in the previous sentence to emphasize that the criteria for the search of research articles included South Africa as an address. This means that at least one of the authors needed to have a South African institution as address affiliation. Importantly, many conservation issues are based in the developing world, where most biodiversity exists, and where many of the global challenges are going to play out, such as the effects of climate change on Africa (De Souza et al., 2015). Many societal challenges relate to inequalities, and solutions should not perpetuate inequalities. There are also power or voice imbalances between science in the Global North vs. the Global South, which unequally influence potential solutions that may be imposed on the Global South (Jeffery, 2014; Carbonnier and Kontinen, 2015). Similarly, gender inequalities highlight the strong voice of men relatively to women in scholarly publications, and the associated lack of participation by women in generating the understanding, and influencing the outcomes and solutions, or non-deliberate exclusion by fellow researchers and/or editorial teams (Webb et al., 2008; Cameron et al., 2013; Fox et al., 2016). In fact, in an article on the ethics of collaborative authorship, Henry (2013) drew an analogy between marital conflict and co-authorship as being among the few relationships that are prone to such hyped interpersonal animosity as when co-authors lose trust and respect for one another; implying that power and partnership can be mutually reinforcing or mutually destructive in the academic world. The reason attributed for such a state of affairs is that authorship in peer-reviewed publications is a highly prized academic reward (Henry, 2013). The trend in the present lion research citations highlights a gender imbalance in terms of the level of recognition that papers with female first authors receive in comparison to their male counterparts. Although more females were first authors and had earned more citations in the 2014–2018 period, none of them have been cited >100 times, indicating a gender imbalance in the level of recognition of female first authors. This imbalance may be the outcome of several underlying causes that could be understood, for instance, by systematically investigating the time frame that female researchers entered the life sciences as scientists/researchers.

Of the published lion studies with an author with a South African affiliation, most of the work was conducted by South African first authors, indicating a strong degree of ownership of that work by the South African research community. Patterns of collaboration have changed, with fewer first author papers coming from European authors, and more from USA authors. The author with the highest number of citations is an Australian national, Matt Hayward, with a total number of citations of 1229 for 11 papers published in the WOS^{TM} database; followed by Funston, P., Slotow, R. and Kerley, G.I.H. who are South African nationals with more than 700 citations each. Interestingly, there are very few first author papers from authors from "Rest of Africa" countries that include a South African-based author, and neither do any African authors figure in the top 20 most cited author list (**Supplementary Material**). Furthermore, the strong presence of South Africa over lion research is emphasized by the fact there are no papers with first author bearing affiliations from the rest of Africa (which includes the range states where lion lives), who have been conducting lion work in South Africa. This indicates that authors from other African countries mainly contribute to research papers as part of a team, and may hint toward a certain degree of North-South power imbalance, or even a power imbalance created from South Africa into the rest of Africa. In today's polycentric world, effective partnerships between northern and southern research organizations are critical to support evidence-based collective action (Obamba and Mwema, 2009; Carbonnier and Kontinen, 2015). Issues of equity, capacity and accountability in multi-disciplinary, multi-national North-South research projects have been voiced in peer-reviewed publications (Henry, 2013; Jeffery, 2014). These can be interpreted in terms of power differentials, but in order to create a roadmap toward effective solutions to improve partnerships, emphasis could be laid on capacity building in key areas that demand attention (Jazeel, 2016). Viewed in a broader perspective, and given the current findings, do we need to shift our intellectual presuppositions about how, who, why, and where lion research is conducted? Based on this line of thought, Nowotny et al. (2003) embed the power differential within the research domain not by using the term North-South which has a high post-colonial discourse as support, but rather by specifying the real issues that occur within research so that the appropriate changes can be envisaged to resolve the disparity. This can be achieved by emphasizing capacity building related to the integration and distribution of knowledge, on the rapidity of transfers toward partners in the South, while at the same time meeting research excellence which is measured through research productivity metrics and scrutinized by funders and employers in academia (Jeffery, 2014). Conservation efforts have transnational range which extend across many countries in Sub-Saharan Africa and West Africa. In order to make lion conservation more efficient and inclusive, capacity building for researchers and practitioners in the rest of the African countries should be prioritized, as well as empowerment of authors from other African countries by South African academics.

Lion conservation research conducted by South Africa is made up of different levels of research collaborative configurations. Mode 1 research has been the predominant form of peer-reviewed scientific outputs generated from the last three decades driven by academic reward in a vicious circle. In recent years, a subtle shift toward Mode 2 research is perceptible whereby accent is being placed on both societal benefit and academic reward within a virtuous circle of research collaboration, implementation and translation. A certain degree of power imbalance has been detected in terms of the relational dynamics pertaining to power. The works of female first authors have a lower impact and academic recognition in the scientific community, as seen in the number of citations that they earn, although the number of female first authors has exceeded the male researchers in the last 4 years. Similarly, the contribution and level of recognition attributed to authors from other parts of Africa is poor. We suggest that authors from other parts of Africa should be empowered by the leading South African researchers to build capacity in conservation efforts, and to reinforce the virtuous circle of research-translation action which is slowly gaining momentum.

AUTHOR CONTRIBUTIONS

RS: conception/design of the work and provide approval for publication of the content. NS and RS: acquisition, analysis or interpretation of data for the work, drafting and revising the work critically for important intellectual content, and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00081/full#supplementary-material

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Improving Human-Lion Conflict Research Through Interdisciplinarity

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Wicked socio-ecological problems are inherently complex and require an interdisciplinary approach for mitigation. Here, we investigated the many drivers of human-lion conflict in East Africa and present a novel conceptual model illustrating the intricate interactions within and between the five main dimensions of conflict. We highlight the importance of broadening research efforts to include these multiple dimensions at all stages of the research process as well as to incorporate higher levels of diversity into research teams. We offer examples and recommendations on how to approach human-lion conflict from a more interdisciplinary perspective. However, challenges exist and will continue to arise as diverse interdisciplinary teams form. We address several main barriers to interdisciplinarity and encourage researchers and institutions to support a team science approach to solving wicked problems like human-lion conflict.

Keywords: conflict, human, interdisciplinarity, lion (*Panthera leo*), team science

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SETTING THE STAGE FOR CONFLICT

Global human-wildlife conflict has increased drastically in recent decades, and the countries of East Africa experience some of the highest rates of conflict in the world. Agonistic interactions are especially severe when involving domestic cattle and African lions (*Panthera leo*) (Franco et al., 2018; Gebresenbet et al., 2018; van Eeden et al., 2018). Cattle are often the most profitable livestock type and losses to lions can have serious financial impacts on livestock-owners (Patterson et al., 2004; Kissui, 2008; Mwakatobe et al., 2013). Moreover, within some traditionally pastoralist tribes, cattle are deeply ingrained in both religious and cultural heritage (Galaty, 1982), and owning cattle in these societies is a feature of communal identity and can be a sign of pride, wealth, and status (Hazzah, 2006; Nkiziibweki and Emmanuel, 2018). Consequently, depredation of cattle is viewed more strongly than loss of any other livestock type and can provoke a retaliatory response among affected people resulting in the killing or maiming of lions perceived to be responsible for these losses (De Iongh et al., 2009; Loveridge et al., 2010; Mponzi et al., 2014; Kuiper et al., 2015). Although the factors that threaten lion survival are many (Treves and Karanth, 2003; Karanth and Chellam, 2009; Maitima et al., 2009; Becker et al., 2013; Lindsey et al., 2013; Everatt et al., 2015), conflict with humans over livestock is one of the most pressing issues affecting lion conservation today (Bauer et al., 2018; Cushman et al., 2018). Reductions in lion populations not only have devastating ecological impacts (Miller et al., 2001; Sinclair, 2003; Ripple et al., 2014) but can also result in huge financial losses for the countries where they reside (Fayissa et al., 2008; Okello et al., 2008). Given the environmental and commercial importance of lions and the cultural and socio-economic significance of cattle in the lives of many livestock-owners, it is essential that sustainable solutions for human-lion conflict be developed and implemented.

Despite the simple label, *human-lion* conflict is far greater and more intricate than a *human vs. lion* competition for resources like cattle. Human-lion conflict is part of a complex coupled human and natural system [often abbreviated "CHANS," an integrated system in which people and natural components inextricably interact (Liu et al., 2007)] which must be understood if the conflict itself is to be addressed. For thousands of years, the East African system has been inhabited by pastoralist tribes that migrate across vast landscapes, herding livestock alongside wildlife, and following seasonal rains (Marshall, 1990; Reid, 2012; Dong et al., 2016). In recent decades however, pastoral lifestyles and ecosystem structure have experienced dramatic changes. Human population growth coupled with subsequent infrastructure and agriculture development have led to large-scale conversion of rangelands (Borjeson et al., 2008; Msoffe et al., 2011). Consequently, many pastoralists have adopted more stationary livelihood strategies in the 20th and 21st centuries (Allsopp, 2009; Western et al., 2009). For nomadic pastoralists, more settled lifestyles contradict many long-held cultural practices with important implications for livestock herd management, livelihoods, and community structure (Homewood et al., 1987; Galvin et al., 2008). The tendency to be more settled, for instance, has changed labor allocation with youth pursuing alternative education and employment options (Tumenta et al., 2013), increased the potential for disease outbreaks deriving from large livestock congregations in confined spaces (Shiilegdamba et al., 2008), and created struggles over access to grazing lands (Fratkin et al., 1999). These evident power structures have been subsequently exacerbated by the establishment of national parks, game controlled areas, and other protected areas (Mbaria and Ogada, 2017). Alternative land-uses like these pay to exist, adding additional monetary pressures for pastoralists to seek occupations not associated with traditionally sustainable livestock husbandry practices (Coast, 2002; Balmford and Whitten, 2003; McCabe, 2003; Kideghesho, 2008). Also, tourism, the primary revenue-generator of protected areas, introduces barriers between local people and wildlife, further diminishing the traditional culture of co-existence held by many African tribes (Rutten, 2002). This can lead to changes in government policies that prioritize wildlife conservation over the livelihoods of pastoralists (Naughton-Treves, 1999). As a result of these changes in landscapes and lifestyles, rates of conflict between people and wildlife, particularly lions and other large carnivores, have increased (Ogutu et al., 2005; Muriuki et al., 2017).

These intricacies position human-lion conflict as a wicked problem. Wicked problems are those that are extremely difficult to manage, have no clear resolution, and typically involve often-competing viewpoints among multiple stakeholders (Rittel and Webber, 1973). Wicked problems cannot be solved using conventional approaches but require partnerships with robust collaboration and transparency among a variety of researchers across the biological, physical, and social disciplines, and may even include arts, humanities, engineering, and new interdisciplinary fields (Berkes, 2004; Rylance, 2013). Collaborative science integrates the vast skills, knowledge, and perspectives needed to fully understand and address wicked problems like human-lion conflict (Eigenbrode et al., 2007). Thus, studying these problems in an interdisciplinary way is integral to improving scientific understanding, which is the first step in the long process of effectively mitigating conflict. Much of the recent research on human-lion conflict has intended to develop sustainable solutions (Santangeli et al., 2016; Broekhuis et al., 2017; Mkonyi et al., 2017; Trinkel et al., 2017), and most conservation programs have multiple objectives, such as protecting biodiversity and improving livelihoods (Game et al., 2014). However, the suggested solutions may not actually be applicable or valid if they do not embrace the complex nature of the problem and the system from the beginning. This paper intends to (i) summarize past literature to highlight the lack of diverse, collaborative partnerships in human-lion conflict research, (ii) explain why this issue may be hampering the success of human-lion conflict resolution efforts, and iii) present a conceptual model to help define this wicked problem and to highlight the need for interdisciplinary research teams.

A RESEARCH EVOLUTION

The first step toward skillful decision making, and in this case conflict resolution, is to define the problem (Keeney, 2004). While wicked problems are notoriously difficult to pin down (Rittel and Webber, 1973), previous studies of human-lion conflict have explained many aspects of the issue, as discussed above. Alone, each study describes a portion of the problem using its own perspective, methods, and narrative. But synthesized, this body of literature shows that human-lion conflict can actually be described by five distinct dimensions. As defined by Montgomery et al. (2018), these dimensions include (1) the carnivore dimension (e.g., the distribution, abundance, and behavior of lions), (2) the livestock dimension (e.g., the abundance, behavior, and husbandry of cattle), (3) the wild prey dimension (e.g., the distribution, abundance, and behavior of wild species that are important prey for lions), (4) the human dimension (e.g., the perceptions, practices, politics, economics, social interactions, and institutions of local people), and (5) the environment dimension (e.g., the land cover, weather, seasonality, and natural resources of the region). Each of these five dimensions is associated with spatial locations where carnivores choose to depredate livestock, and each can drive the conflict individually as well as in combination. Thus, human-lion conflict is comprised of complex layers of interacting factors within and between the five main dimensions. Here, we devised a novel conceptual model, including just some of the countless interacting factors, to illustrate the interconnectedness of all five dimensions and the complexity that is inherent to human-lion conflict (see **Figure 1**). While the model does not intend to include every aspect necessary to manage or mitigate conflict, it can be used to more fully comprehend the various factors that lead to actual occurrences of conflict and therefore to identify the types of expertise needed to address each.

Despite this complexity, human-lion conflict has historically been viewed rather narrowly within the scientific community. Montgomery et al. (2018) reviewed all studies of human-lion

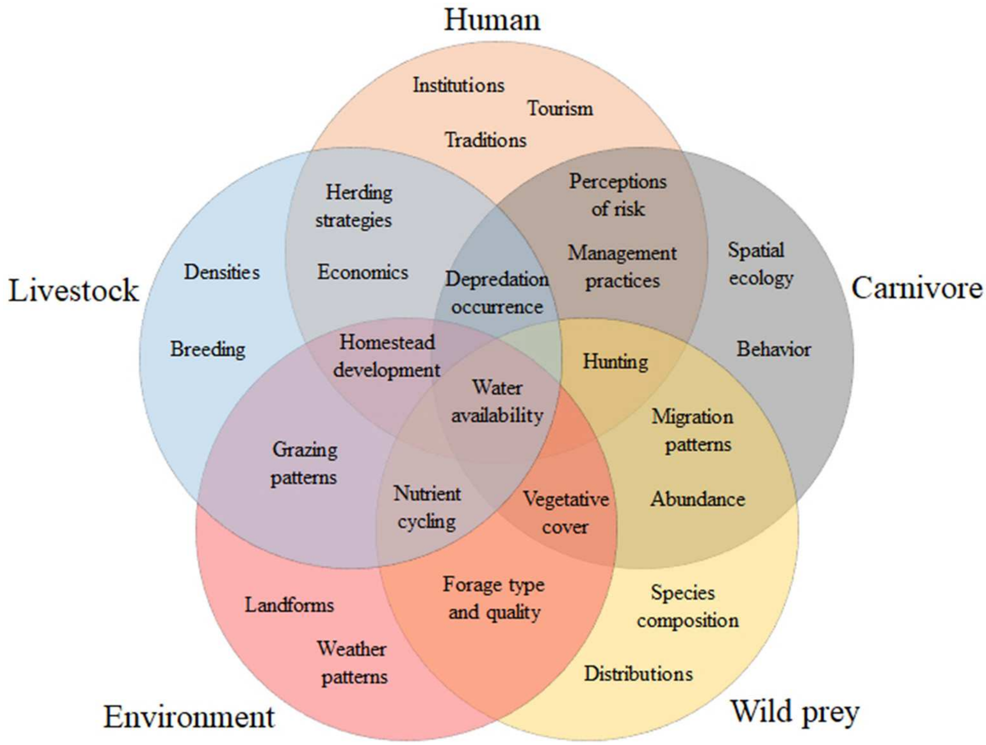

FIGURE 1 | A model for human-lion (*Panthera leo*) conflict composed of five distinct and overlapping dimensions. A non-exhaustive list of factors within and between dimensions is presented.

conflict published between 1990 and 2015 and found that the majority of papers studied only one or two dimensions at a time, with the most common dimension studied being the human. None of the studies assessed all five dimensions simultaneously. Thus, despite the fact that research on human-lion conflict has grown exponentially since 1990, that research has had quite low levels of interdisciplinarity. Unfortunately, this lack of interdisciplinarity lies in striking contrast to the multidimensional and interrelated nature of the conflict itself and the system in which it lies, suggesting that any proposed solutions or recommendations have not taken into consideration all of the aspects of the initial problem. While it may be impractical to include all interrelationships in any one study, beginning with a systematic examination of the problem will promote communication on crucial problem features and ensure that important dimensions are not omitted (Keeney, 1982).

Just as the five dimensions of human-lion conflict overlap and interact in the model presented in **Figure 1**, so too should the research avenues pursued in the development of solutions. We contend that the complexity of human-lion conflict, as is the case with other wicked problems, is too vast to be effectively evaluated independently. Connections must be forged within the broader community of scientists to form new and flexible working teams (Norris et al., 2016). Therefore, we recommend that researchers invite interdisciplinary experts to collaborate in a team-science approach where all individuals engage in the definition of the problem and then the design, implementation, and analysis of multifaceted research programs (Stokols et al., 2008; Bennett and Gadlin, 2012). We suggest that the unique hypotheses and methodologies of each separate research dimension inform and support the others and that the scope and scale of each dimension is periodically reevaluated by the team. Overall research objectives must continue to evolve as more data is collected and results determined. In this way, the constant interaction, adaptation, and evolution of a team's work is integral to its interdisciplinarity. Without this vital component, a research initiative may be multidisciplinary but never truly interdisciplinary, or even transdisciplinary (Eigenbrode et al., 2007; Miller et al., 2008).

Within the context of human-lion conflict, the possible interdisciplinary research pathways are innumerable. For example, a team may want to determine if and how cattle behavior is affected by the risk of lion attack. Before designing a study of this type, we recommend that the research team work to identify the ways in which the five dimensions might interact to develop patterns of human-lion conflict. Thereby, the team would need to consider, for example, if the densities of wild prey species vary across their study sites, if all cattle herds have equal access to water sources, or if herder age or tribe affiliation may impact herding strategies. This would likely require the involvement of professionals from multiple disciplines. After data collection and analysis, the team's results would also have important implications for all five dimensions of conflict. Cattle behavior might directly impact the vegetation and soil within the grazing areas, and the team could use this information to identify habitats at risk of overgrazing, erosion, and land cover change. Through discussion and interpretation of the results, this environmental data might then feed back into the design of research questions associated with the human dimension, such as how local livelihoods are impacted by habitat degradation and environmental uncertainty. Thus, this version of interdisciplinarity provides an example of a research model that inherently examines interactions among the five dimensions before, during, and after the research is conducted and incorporates constant reevaluation of the problem by a variety of collaborators.

BUILDING BLOCKS OF AN INTERDISCIPLINARY TEAM

Montgomery et al. (2018) not only found that studies of human-lion conflict lacked diversity in their research design, but also in their co-authorship. Studies tended to have just three co-authors, most of whom derived from three highly related fields (biology/ecology/zoology, wildlife management/conservation, and environmental science). Additionally, although the human dimension was the most commonly studied component of human-lion conflict, only 4% of papers included co-authors from social science or humanities-based disciplines. Furthermore, less than a quarter of papers had authors from two or more disciplines. These metrics demonstrate again that human-lion conflict research exhibited low levels of interdisciplinarity. Similarly, Bauer et al. (2019) found an extreme lack of diversity in race, gender, and nationality of scientists conducting and publishing lion research (Bauer et al., 2019). Team diversity (in expertise, race, gender, education levels, skillsets, etc.) is a necessary attribute of interdisciplinary research and has been positively correlated with the performance of teams, as measured in a multitude of ways (Bennett et al., 2010; Read et al., 2016). For example, as team diversity increases so too does the frequency of team communication, the creation of more creative problem-solving strategies, and the implementation of higher quality decisions (Milliken and Martins, 1996; Hall et al., 2008). When these collaborations are successful, their accomplishments surpass those of any one individual (Cheruvelil et al., 2014). Thus, as more diverse teams develop, they could hold the potential to change the way human-lion conflict is studied and, ultimately, managed.

The foundation of a diverse interdisciplinary team is the makeup of the team members themselves. Here, this refers not only to each individual team member's core disciplines, but also their personal histories, beliefs, and skillsets. A team formed of people from diverse educational and professional backgrounds should perform better than one from homogeneous backgrounds given their broader range of perspectives and knowledge from which to draw (Eigenbrode et al., 2007; Bell et al., 2011; Norris et al., 2016). Also, a team with a mix of new and tenured members should be more innovative as a result of the combination of fresh ideas and established experience. Therefore, we recommend teams not only increase representation of scientists from diverse disciplines, but also from diverse backgrounds, cultures, ranks, and education systems, as well. Thus, an effective interdisciplinary team studying human-lion conflict in East Africa, for example, might include native African scholars, team members from around the world, seasoned experts, innovative young professionals, graduate students, those with knowledge in ecology, biology, anthropology, geology, communications, history, political science, and more.

Though examples of these types of teams are becoming more common with NGOs (such as San Diego Zoo Global) and within government agencies (see the European Commission's Horizon 2020 projects or the National Science Foundation's Long Term Ecological Research Network), support for this strategy within academia is comparatively rare. We know of no current interdisciplinary academic teams publishing research on all five dimensions of human-lion conflict. One exemplary case from a different wicked problem, however, can be found in an interdisciplinary study of the Turkana people of Kenya. For over a decade, a team of ecologists, anthropologists, nutritionists, and others conducted intensive research aiming to understand human-environment interactions in grassland ecosystems (Leslie and Little, 1999). Through their research, the team determined that policies promoting the settlement of nomadic peoples were ill-informed, as the Turkana had developed sustainable land-use strategies through changes in diet, mobility, and political relations (Galvin, 1992; Leslie and Little, 1999; McCabe, 2010). This is a superb example of academic interdisciplinary research from a diverse team that was able to produce novel research outcomes from a complex coupled human and natural system. Remarkably, one consideration left out of this long-term study is the role of wildlife populations on the rangelands, especially wild ungulate species and large carnivores. Thus, despite this example, important gaps in our knowledge of these systems still exist. Nevertheless, we believe interdisciplinary teams are best suited to embrace challenges and fill the voids inherent to the pursuit of wicked problems. We recommend that future research builds on the work of this team and others, utilizing a clear conceptual model to more fully define and understand each unique dimension of their wicked problem and to incorporate the knowledge and skills needed to study them appropriately.

A CHALLENGE WORTH PURSUING

While our focus has been on highlighting the ways that increased interdisciplinarity and diversity could improve human-lion conflict research specifically, these concepts would benefit researchers studying other complex wicked problems as well. However, even with a clear but flexible definition of the problem, the guidance of a conceptual model, and an open-minded team, it is crucial to remember that there are no quick fixes for any of the complicated conservation issues emerging today. For example, interdisciplinarity is a time-consuming endeavor that may reduce short-term productivity given the extra time commitment and effort required (Pennington, 2008; Goring et al., 2014; Kwon et al., 2017). However, despite this early investment of time, as confidence is established within long-term partnerships, the process becomes quicker and can yield higher productivity with time (Jakobsen et al., 2004). Studies have shown that interdisciplinarity increases long-term citation rates, which boosts the visibility of scholarly work and reflects its usefulness and influence (Wang et al., 2015; Leahey et al., 2017). Thus, we encourage emerging interdisciplinary teams to have patience and a clear vision of their long-term goals. Additionally, team leaders can foster morale and a sense of accomplishment by rewarding research outcomes above and beyond publications (Goring et al., 2014), and professors can encourage interdisciplinarity in their classrooms to prepare young scientists for the rigors of such collaborations.

Another possible barrier to successful interdisciplinarity is intra-team variation in theoretical constructs, judgements, and world-views, which are often directly linked to the personal values of the individuals (Lélé and Norgaard, 2005). Within the context of solving wicked problems, team members may have differing opinions on which aspects of the research are of greatest importance to society, and which are most relevant to the scientific evaluation of the problem. Furthermore, there can often be a lack of familiarity with the terminology, methods, and underlying assumptions of the various disciplines involved and a difficulty with properly communicating these terms (Heemskerk et al., 2003; Jakobsen et al., 2004). We recommend that team members attend yearly face-to-face research summits during which all proposed methodologies, research expectations, and current results are presented and discussed. Direct engagement between group members is one of the greatest predictors of productivity (Pentland, 2012), and it is through interaction and communication that trust is built within a team (Bennett et al., 2010). Therefore, we suggest that team leaders take an active role in fostering trust within the group rather than hoping it will evolve over time. Teams should hold open discussions on often-difficult topics such as authorship practices, conflict resolution strategies, and individual expectations in order to overcome challenges relating to personal values and to achieve mutual understanding. Other networking opportunities such as scientific conferences should also become more interdisciplinary in their design to facilitate communication across disciplinary boundaries and to inspire novel thinking and creative partnerships. University faculty and administrators can take an active role in breaking down barriers to interdisciplinarity by making efforts to align performance evaluations to facilitate reward systems among interdisciplinary colleagues, diversifying course offerings, and by encouraging enrollment in non-major science courses or experiential learning activities. Providing young scientists with opportunities for cross-disciplinary scholarship early in their careers will not only equip them with the tools needed to understand and incorporate diverse philosophies into their work, but doing so also has the potential to stimulate future research in ways currently unimagined.

Finally, another challenge for interdisciplinarity is cost. There are several ways to be interdisciplinary: one in which each team member is an expert in their discipline and collaborates with other experts in other disciplines through the mechanisms discussed here, and another in which each team member seeks to attain a certain level of individual interdisciplinarity in their training so as to approach the research from multiple perspectives (Frodeman, 2010). The latter mode may be costlier, as it requires each team member to acquire a great deal of knowledge of the other collaborating fields. The former mode, however, is more challenging for putting the interdisciplinarity into operation and thus may require increased time and additional communication between members, adding to costs more indirectly (Hunter, 1999; Moran and Ostrom, 2005). Each team leader should be aware of these alternatives, and consider all options when building, maintaining, and funding an interdisciplinary team [one great resource for leaders and team members alike is the National Institute of Health's Collaboration and Team Science Field Guide Bennett et al., 2010]. Additionally, a recent study showed that research proposals with higher levels of interdisciplinarity were less likely to be funded (Bromham et al., 2016). Thus, institutional-level changes need to be made to promote and finance interdisciplinary work.

BRINGING INTERDISCIPLINARITY INTO THE FUTURE

In our increasingly globalized world, international collaborations are predicted to increase across scientific fields (Hall et al., 2008) and younger generations of PhD students are already showing higher proportions of interdisciplinary academic backgrounds than prior generations (Haider et al., 2018). Unfortunately, formal training for scientists and graduate students on how to successfully collaborate within large teams remains rare (Cheruvelil et al., 2014; Elliott et al., 2017). Increased training is needed as well as increased institutional support and funding for diverse teams that may require additional time and specific skills. We also recommend that additional research attention be devoted to evaluations of the factors that correlate with team success for interdisciplinary teams studying wicked problems and to create best practices on how to establish these teams over time. Conceptual models like the one presented here on the five dimensions of human-lion conflict can help interdisciplinary teams to better define, visualize, conceptualize, address, and readdress each dimension of their work as they move forward.

The challenges described here are just a few of many that face interdisciplinary teams. However, they are not insurmountable and interdisciplinarity still holds immense promise for the development of effective solutions to human-lion conflict. Disciplinary studies on aspects of one dimension of conflict only (e.g., local people's perceptions of depredation risk, or carnivore movement patterns) will continue to provide important scientific facts needed when designing conflict mitigation efforts. However, these efforts rely not only on credible science but also on creating an environment in which people can express their views and values through professional collaborative processes (Gregory et al., 2012). Seeking quick fixes often disregards multiple perspectives and dimensions of the problem (Rust et al., 2016) and this is likely a contributing factor as to why East African lion numbers continue to fall. Lions are among the most scientifically studied wild felid species (Brooke et al., 2014), and levels of conflict with humans have been considered "severe" for over a decade (Inskip and Zimmermann, 2009). Thus, lions are in a unique position in that the conflict is widely studied (Montgomery et al., 2018) but sustainable solutions are not yet forthcoming. We believe that oversimplified explanations proposed through homogeneous research efforts do not hold the power to solve wicked problems situated within complex systems. Thus, there is productive space for team science to test the ways in which diverse, interdisciplinary research might be better placed to identify, validate, and scale novel solutions for human-lion conflict as well as other wicked problems. We encourage researchers to build capacity at local levels and increase data sharing so that the results of future research can be actively implemented in solving these problems (Caron and Serrell, 2009). Civil scientists, non-governmental organizations, local communities, and traditional ecological knowledge should be incorporated into studies whenever possible, in pursuit of the ultimate goal of transdisciplinarity. This paper is intended to be used as a stepping stone toward this goal offering a new conceptual model, examples, and advice that research-informed conservation teams can draw upon when beginning the process of transitioning out of scientific "silos" and moving toward a more integrative approach to research. In this way, we hope to encourage new conservation norms where the process of solving wicked problems like human-lion conflict is not in itself a wicked problem.

AUTHOR CONTRIBUTIONS

JB and RM were the project leaders and conceived and participated in every portion of the manuscript development. ML aided in the original development of the manuscript frame and provided additions and edits to the manuscript. TM contributed significantly to writing and editing the manuscript.

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The African Lion: A Long History of Interdisciplinary Research

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Over the past 50 years, lion research has covered a wide range of interdisciplinary topics involving extensive collaborations with scientists from over a dozen different fields. These collaborations have not only led to greater scientific understanding of disease dynamics, impacts of sport hunting on lion populations, and the interactions of lions and their prey, but also resulted in a large-scale disease-control program in rural Tanzania, new hunting policies in several African countries, widespread adoption of camera-traps as a conservation-management tool, new statistical and economic approaches to broadscale conservation approaches, and innovative local-level conservation interventions.

Keywords: lions (*Panthera leo*), collaborative research, interdisciplinary studies, long-term studies, conservation

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Lions (*Panthera leo*) have provided key insights into the ecology of large carnivores, and, as they have become increasingly threatened by human population growth, lions have inspired a wide variety of conservation strategies with wide relevance for protecting other endangered taxa. But compared to other large carnivores, lions were, until recently, reasonably abundant and, compared to their forest-dwelling counterparts, they are easily observed. Thus, the lion has attracted more behavioral, ecological and conservation-related research than any other African carnivore. An essential aspect of this research history is the fact that lions have long been the subjects of interdisciplinary investigations, and this multi-pronged approach has attracted scientists from numerous fields to work with lions and, in many cases, apply their knowledge to other species. Having led the Serengeti Lion Project for nearly 40 years, I have been privileged to participate in much of this work.

THE BASICS OF LION BIOLOGY

When George Schaller started the Serengeti Lion Project in 1966, he relied on binoculars, field notebooks and a Land Rover to observe the lions in their natural habitat. His efforts became the basis of his landmark book, *The Serengeti Lion*, which won the National Book Award (Schaller, 1972), and, after taking over the project in 1978, Anne Pusey and I initially followed the same path, though by this point, we were interested in testing specific hypotheses about the behavior of this famously sociable species. Brian Bertram, David Bygott, and Jeannette Hanby had maintained detailed data on hundreds of individuals between 1969 and 1978 (Bygott et al., 1979), so we were able to take advantage of 12 years of demographic data to investigate the effects of kinship on cooperation and competition within male coalitions (Packer and Pusey, 1982; Grinnell et al., 1995), dominance and aggressive feeding competition at kills (Packer and Pusey, 1985; Packer et al., 2001), and communal nursing (Pusey and Packer, 1994). In brief, first, while large male coalitions are always composed of close relatives, pairs and trios include non-relatives that cooperate as whole-heartedly as close kin; second, while larger age-sex classes generally dominate smaller ones at kills, within each age-sex class lions follow an "ownership rule" whereby adult females, for example, do not displace other females from feeding sites at the carcass; third, females that give birth within a few months of each other raise their cubs together in a "crèche," wherein mothers nurse each other's cubs according to the size of their own litter and their kinship to the other females.

As can be seen from the dates of these publications, behavioral research on lions can be extremely time consuming. For example, our non-offspring nursing paper required nearly a dozen years of field work before we could obtain an adequate sample size. Thus, as our initial funding shifted from the Harry Frank Guggenheim Foundation (whose mandate is to explore the relevance of animal behavior to a broad understanding of violence, aggression and dominance) to the National Science Foundation (whose mandate is to support fundamental research in the non-medical fields of science and engineering), we broadened our focus to include a variety of topics in behavior, ecology and evolution—while remaining an overall commitment to conducting *basic* research for the following 31 years of NSF support.

But starting in 1984, we partnered with geneticists and reproductive physiologists at the National Cancer Institute and Smithsonian Institution to evaluate levels of inbreeding in the small naturally isolated lion population in the nearby Ngorongoro Crater by comparing genetic profiles of these animals with individuals from the large panmictic Serengeti population (O'Brien et al., 1987; Packer et al., 1991a). The Crater lions not only showed lower levels of genetic diversity, but they also displayed many of the same physiological signs of chronic inbreeding as inbred strains of domesticated animals (Wildt et al., 1987; Brown et al., 1991; Munson et al., 1996). Genetic studies have since become common in large carnivores (e.g., Johnson et al., 2010; Hedrick et al., 2014) and have grown greatly in scale, even inferring regional-scale bottlenecks in lion populations caused by persistent persecution over the past two centuries by European settlers (Dures et al., 2019).

As DNA fingerprinting became available in the late 1980s, we were one of the first field projects to assess paternity and kinship coefficients (Gilbert et al., 1991) and to relate these findings to evolutionary theories about cooperation and reproductive skew (Packer et al., 1991b). The resident males in our sample fathered 100% of the cubs conceived during their tenure, and littermates were almost always full siblings. While female lions are egalitarian, with each pridemate enjoying similar reproductive rates as her sisters, daughters, cousins and aunts, male coalition partners suffer increased reproductive disparities with increasing coalition size—and individual males only team up with unrelated partners to form pairs and trios; male quartets and larger are composed entirely of brothers and cousins. Rigorously investigating the genetic structure of social groups soon became common in birds, social insects and primates (Ross, 2008), but we got off to an early start during a time when molecular studies were still extremely costly—thanks to the charismatic appeal of the lion to a well-funded genetics lab at the National Cancer Institute (O'Brien, 2003).

From this large archive of blood samples, we discovered that large felids were infected with feline immunodeficiency virus (FIV_{PLE}, Olmsted et al., 1992), but coupled with our long-term demographic data, we found that lions did not suffer serious illness despite life-long infection with the virus (Brown et al., 1994). These findings inspired parallel research on a similar virus, FIV_{PCO}, in pumas. Experiments with domestic cats have shown that prior exposure with either FIV_{PLE} or FIV_{PCO} is immunoprotective against FIV in domestic cats (VandeWoude et al., 2002).

We used the Tanzanian lion samples to conduct epidemiological studies of the large-scale die-offs in the Serengeti and Ngorongoro Crater in 1994 and 2001 respectively (Roelke-Parker et al., 1996; Packer et al., 1999; Munson et al., 2008). We eventually determined that canine distemper virus (CDV) was part of a diffuse multi-host system and that CDV was only lethal in the lions when co-occurring with high levels of the tick-borne parasite *Babesia* (Munson et al., 2008). We also used the CDV outbreak as a disease "challenge" to test whether carriers of different strains of FIV_{PLE} experienced different outcomes from exposure to the morbillivirus, and, indeed, individuals infected with the B-clade of FIV_{PLE} suffered higher mortality than carriers of the A or C clades in the Serengeti outbreak (Troyer et al., 2011). Thus, the lions have played a role in the growing study of co-infections and viral communities (Fountain-Jones et al., 2019).

As a direct result of the CDV outbreaks, Sarah Cleaveland, Andy Dobson and I established the "Carnivore Disease Project" with funding from the NSF program in the Ecology of Infectious Diseases. The CDP simultaneously monitored disease status in the Serengeti/Ngorongoro lions and the domestic dogs that live in villages surrounding the Serengeti National Park and within the Ngorongoro Conservation Area. The project has inoculated around 50,000 dogs per year starting in 2002 (Czupryna et al., 2016). The wild dogs (*Lycaon pictus*) in the Serengeti had suffered from periodic disease outbreaks in the 1960s and rabies was positively diagnosed in 1990 (Gascoyne et al., 1993). But it wasn't until the lion outbreaks that we were able to assemble an interdisciplinary team of veterinarians, ecologists and mathematical modelers to gain the necessary funding to protect endangered wildlife and rural villagers from rabies (Hampson et al., 2009), as well as to reduce the impacts of CDV (Viana et al., 2015). Indeed, the CDP served as a proof-of-concept effort that directly led to even larger-scale dog vaccination programs in low- and middle-income countries in Africa and Asia (Cleaveland and Hampson, 2017).

Around the turn of the millennium, we worked with dermatologists and physiologists to study the lion's mane (West et al., 2006). We also collaborated with a Dutch company called International BonTon Toys, whose staff constructed a set of life-sized lion dummies and enjoyed their newfound freedom to sculpt lifelike models instead of cute toys. A series of pairwise tests showed that females clearly preferred dark-maned dummies and a somewhat milder preference for long-maned dummies, whereas males preferred to challenge lighter- and shorter-maned dummies (West and Packer, 2002). Thanks to the FLIR Corporation's loan of an infrared camera, we found that dark-maned males suffered greater heat stress (black mane hair is thicker than blond). The dark-maned males enjoyed greater survival and reproductive success; thus, the lion's mane appears to be an honest indicator of being able to take the heat, rather than as a shield to protect the head and neck against wounding (West et al., 2006). Amusingly, our work inspired several investigations into the function of the male beard in humans (Blanchard, 2010; Dixson and Vasey, 2012).

Lions being highly infanticidal, frequent removal of resident males by sport hunters could have potential knock-on effects on the entire population. Thus, we worked with a team of computer scientists to develop a program, SimSimba, that established guidelines for "harvesting" lions in a sustainable manner (Whitman et al., 2004). The dynamics of lion populations could only have been addressed through a comprehensively parameterized simulation model using long-term data from the Serengeti field study, yet the key insight from these simulations was surprisingly simple: hunting impacts could essentially be eliminated by restricting offtakes to males above 6 years of age. The 6-year minimum is now official government policy in Mozambique, Tanzania, Zambia and Zimbabwe, and our subsequent work (Packer et al., 2009) has directly inspired similar rules for leopard hunts in South Africa (Balme et al., 2012) and further refinements for lion offtakes in poorly protected areas like Zambia (Creel et al., 2016).

Shortly after the development of SimSimba, we were asked by the Tanzanian Government to investigate a serious outbreak of man-eating lions in southern Tanzania (Packer et al., 2005) and subsequently worked with geographers and social scientists to better understand the local risk-factors leading to greater levels of human-lion conflict (Kushnir et al., 2010, 2014). We found that local people endangered themselves by sleeping in the open during harvest time to protect their subsistence crops from night-time incursions by bush pigs—the lions' primary prey in the region. Although people accurately rate their relative risks of lion attacks in different contexts, their fear of lions is greatly exaggerated in comparison to the risks from disease or malnutrition (Kushnir and Packer, 2019). The sheer scale of the Tanzanian outbreak (900 cases in 15 years) permitted the application of epidemiological techniques for predicting the approximate timing and location of further lion attacks and proved useful for characterizing attacks by tigers and leopards in India and Nepal (Packer et al., 2019): lion outbreaks include more victims, cover a broader geographic area and persist for longer periods than in the other two species. Modeling routine reports of carnivore attacks with the SaTScan software could potentially provide an early warning system in any affected area and could also be applied to attacks on livestock as well as on humans.

Most recently, we broadened our monitoring of the Serengeti lions to include all the larger vertebrates in a 1,100-km^2 portion of the long-term study area (Swanson et al., 2015). In developing methods to process and analyze millions of photographs from our SnapshotSerengeti grid of over 200 camera traps, we worked with a citizen-scientist platform

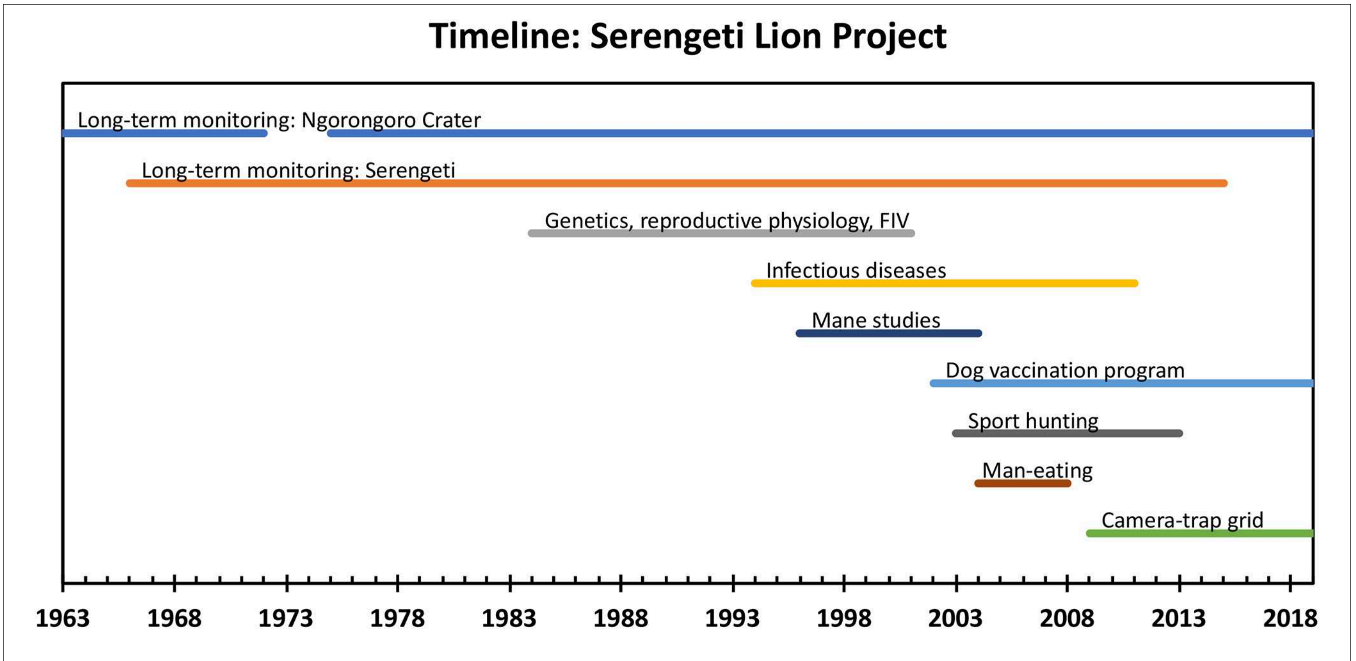

FIGURE 1 | Sequence of activities between 1963 and 2018. Continuous monitoring of the Serengeti lions began in 1966; retrospective monitoring of the Crater lions was achieved by soliciting photographs from staff, tourists and scientists who spent various periods of time in the area between 1963 and 1972; continuous on-the-ground monitoring began in 1975. The genetics, physiology and retrovirus studies were conducted in collaboration with the Laboratory of Viral Carcinogenesis and the Smithsonian. Infectious disease studies were performed with vets from the US and Switzerland. The mane studies involved assistance from a Dutch toy company, American dermatologists and the makers of an IR camera. The dog vaccination program was initiated in collaboration with vets from the UK and continued by an American zoo and US vet school. The sport-hunting work was developed in cooperation with computer scientists and Tanzanian wildlife authorities. The man-eating studies involved the Tanzanian government and American social scientists. The large-scale camera-trap work was implemented in collaboration with an online Citizen Science platform, The Zooniverse.

called the Zooniverse, several database managers, computer scientists and Bayesian statisticians to turn a mountain of individual images into a holistic picture of species relationships in the Serengeti (Anderson et al., 2016), species co-existence of large carnivores (Swanson et al., 2016) and even how prey balance predation risks with foraging success over each night of the lunar cycle (Palmer et al., 2017). The huge archive of labeled images also allowed for the development of new methods for computer-based image recognition (Norouzzadeh et al., 2018). The success of SnapshotSerengeti has so far resulted in over 40 different camera-trap projects on Zooniverse, and we have recently expanded the original project to become SnapshotSafari (see www.SnapshotSafari.org), which provides species classifications for dozens of camera-trap grids in multiple African countries with the ultimate goal of helping wildlife managers assess the population status of the lions' primary prey species in their respective reserves (see Palmer et al., 2018).

FROM ECOLOGY TO CONSERVATION BIOLOGY

Working deep inside one of the best protected parks in Africa, we had only rarely been confronted with the realities of lion conservation: lions can cause considerable harm to local communities, and people can be quick to retaliate. But around the year 2000, I began to hear reports of lions being killed by local people in the Ngorongoro Conservation Area, at the eastern edge of the long-term Serengeti study area. I asked Dennis Ikanda to survey Maasai communities across the NCA, and he found that lions were being speared both in retaliation for livestock depredation and for ritual purposes (Ikanda and Packer, 2008). Around the same time, Tanzanian National Parks asked me to spend time in Tarangire National Park as lion numbers appeared to be declining across the Maasai Steppe. My graduate student, Bernard Kissui, soon confirmed widespread retaliatory lion killings that likely drove a 25% decline in lion numbers (Kissui, 2008). By the time the Tanzanian Government asked us to investigate the extensive outbreak of man-eating lions between Dar es Salaam and the Mozambique border, it was clear that lions presented enormous threats to human safety and livelihoods all across the country, and the situation was likely similar across Africa, wherever lions still roamed.

The continentwide lion conservation crisis clearly required information from as many populations as possible—and my collaborations initially changed from interdisciplinary to geographical. We needed real data on the current status of lions across all of Africa, we needed to know if population trends were up or down, and we needed to investigate why some populations appeared to be thriving while so many others were in trouble. Loveridge and Canney (2009) had recently developed methods for estimating carrying capacities for lions, based on soils, rainfall and prey abundance, so I assembled survey data from over 40 field biologists to compare the "real" with the "ideal" (Packer et al., 2013). The results fell into two broad categories: lions living inside fenced reserves were always close to the predicted ecological limits, but virtually none of the unfenced reserves were even close to their potential. Most lions reside in unfenced areas, and two key factors predict their population status: first, lions fare best in areas with low human population density—think Namibia, Botswana or other desert countries. Second, lions thrive in parks with management budgets of around \$1,000–2,000/km^2/year; many reserves in Africa are little more than "paper parks" with budgets of only a few dozen dollars per square kilometer per year.

The Dollars and Fence paper provided the direct impetus for utilizing Bayesian techniques for estimating population trends from limited survey data rather than relying on simple extrapolations (Bauer et al., 2015), and our analysis provided the basis for the widely quoted statistic that "Africa has lost nearly half of its lions in the past 25 years" and also informed the USFWS decision in 2016 to classify the western subspecies of lion (*P. l. leo*) as "endangered" and the rest of Africa's lions (*P. l. melanochaita*) as "threatened." Our initial economic analysis for estimating "how much it costs to conserve a lion" similarly inspired a more comprehensive effort to determine the true costs of lion conservation (which also worked out at ∼\$1,000/km^2/yr) (Lindsey et al., 2018). Similar statistical and economic approaches will eventually become the norm for any other well-studied, widely distributed species—but the lions came first.

While the Serengeti lion study drew researchers from a dozen different fields (see Timeline in **Figure 1**), conserving the species for the next 50 years will require even greater inputs from social scientists, political scientists, economists and geographers. Indeed, some of the most promising programs promoting human-lion coexistence (the so-called "Lion Guardians") invest far more energy on people than lions (Hazzah et al., 2014), and nearly a dozen similar projects are now underway in Kenya, Mozambique, Namibia, Tanzania, and Zimbabwe (e.g., Lichtenfeld et al., 2015; Western et al., 2019).

The lion is one of the most dangerous wildlife species in the world. What we learn from lions will surely inform conservation practices of multiple species worldwide. By its nature, the in-depth study of any single species, conducted long enough, becomes interdisciplinary.

ETHICS STATEMENT

All the studies involved in this review were published with reported IACUC permit numbers. No new data were included in this paper.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Asiatic Lion: Ecology, Economics, and Politics of Conservation

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Asiatic lions typify most challenges faced by large carnivores: single population, historical bottlenecks, habitat loss, poaching, and conflict with humans. Their recovery from <50 in a few hundred km^2 to >500 occupying 13,000 km^2 of agro-pastoral Saurashtra landscape, Gujarat, India is an enigma. We review and evaluate the multidisciplinary aspects of lion conservation-strategy that covers ecology, conflict, community perceptions, economics, management, and politics. The history of modern lions in India dates back to ∼4–6,000 BP, but evidence suggests presence as early as 10–15,000 BP. Asiatic lions can be distinguished from African lions by their belly-folds; adult males and females weighing 160 (SE 4.7) and 116 (SE 3.7) kg, respectively. Lion density ranged from 2 to 15/100 km^2 in the Saurashtra landscape. Demographic parameters of Asiatic lions were comparable to African lions. Prides were related females and cubs; males lived separately in hierarchical coalitions having overlapping ranges with multiple prides. Lionesses mated with multiple coalitions to reduce infanticide and enhance genetic diversity of their progeny. Few hectares of scrub sufficed as daytime refuges, while >4 km^2 patches were required for breeding. Sink populations outside Gir Protected Area (PA) were maintained by immigrants. Lions within PA fed primarily on wild-prey, while scavenging and predation on livestock was the mainstay outside. Monetary compensation for livestock-depredation, legal-protection, lion-related profits, combined with religious and cultural sentiments were major drivers of population recovery. The lion has become a socio-political instrument in Gujarat, which despite a Supreme Court directive, has not parted with founders to establish another population. Threats from epidemics loom large and currently a canine distemper virus outbreak is prevalent. Attacks on humans were rare, however, with increasing lion density the intensity of conflict is increasing. This, coupled with lowered tolerance of communities due to erosion of traditional values sets the stage for retaliation. Future of lions outside PA is uncertain as breeding refuges and their connecting corridors are vanishing rapidly. A human-free National Park of ∼1,000 km^2 is essential for ensuring a viable population that retains its ecological role and evolutionary potential. Legalizing lion based ecotourism by forming village consortia holds promise to prevent land conversion and promoting lion-human coexistence.

Keywords: conservation policy, Gir, human-carnivore conflict, long-term research, reintroduction

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INTRODUCTION

Unprecedented human expansion and consequent resource exploitation in the last two centuries have sheared the range and imperiled the survival of biodiversity globally (Ripple et al., 2014). Large carnivores as a taxa are most affected because by virtue of being apex predators they need large ranges, occur at low densities and compete with humans for space and food, prey on livestock and sometimes on humans; bringing them into direct conflict with human interests (Ceballos and Ehrlich, 2002). In the ushering Anthropocene, the fate of biodiversity depends on how well species and humans adapt to live alongside each other. In densely populated developing countries, conservation of pristine wilderness is a luxury and many protected areas have human habitations within them (Rangarajan and Shahabuddin, 2006). The paradigm of coexistence seems to be the only solution for several carnivore populations wherein local communities either have a high level of tolerance or even *encourage* carnivore population buildup, while carnivores "learn" to live with people (Ripple et al., 2014). The major challenges faced by mega-biodiverse countries like India in conserving their natural heritage are: high human density (1.2 billion people with an average human density of 382 people/km^2; Human Census Report 2011, Government of India available at www.census2011.co.in), poverty, agrarian economy, and rapid development (Karanth and DeFries, 2010). Though 5% of India's geographical area is secured as Protected Areas (PAs), these PAs are small (average size of <300 km^2), with several of them having human settlements and varying levels of anthropogenic activities within them (Rodgers et al., 2003). Furthermore, the PA network is severely fragmented by intervening human-modified landscapes, resulting in poor habitat connectivity (Qureshi et al., 2015). Such a scenario creates wildlife populations that are vulnerable to extinction through demographic and environmental stochasticity (Soulé, 1987), and a high potential for human-wildlife conflict (Madhusudan and Mishra, 2003; Banerjee, 2012). It is indeed surprising that despite these odds, with the exception of the Asiatic cheetah (*Acinonyx jubatus venaticus*) India has not lost its large carnivore assemblage since written history (Divyabhanusinh, 1995). This can primarily be attributed to the historical, religious, and cultural reverence for life forms in majority of the Indians (Gadgil and Thapar, 1990; Dorje, 2011; Renugadevi, 2012). However, with the current escalation of habitat loss due to the "green revolution" in agricultural practices, other developmental activities as well as erosion of traditional values; conservative estimate suggests that 20% of large mammalian fauna in India may face extinction, and several species have already disappeared from over 90% of their original range (Madhusudan and Mishra, 2003; Karanth et al., 2010).

The charisma of lions (*Panthera leo*) on the human psyche is historical (ingrained in the Vedas and Homer's Iliad) and continues into the modern era. Lions have dominated our association with large carnivores particularly because they represent an elemental survival strategy which is very akin to ours- "living in groups". From pre-historic war emblems satisfying royal egos to motion pictures catering to young minds like the Lion King, from the notoriously vicious man-eaters of Tsavo to the famed controversy surrounding *Cecil* getting shot that kindled empathy across the world; lions have seesawed between the notions of charismatic and loved to being hated and persecuted (Macdonell, 1897; Patterson, 1907; Macdonald et al., 2016; Carpenter and Konisky, 2017; Kostuch, 2017).

Asiatic lions (*P. l. persica*) that once ranged from Persia to eastern India are now restricted to a single population in the Gir-Saurashtra region of the state of Gujarat, Western India. This single population was established from a small founder, shares space with humans across almost all of its range and therefore typifies major challenges that large carnivore conservation can potentially face (Johnsingh et al., 1998). While global debate surrounds the issue of whether lions can be effectively conserved outside PAs (Packer et al., 2013; Stephens, 2015); in India the Gir National Park of only 259 km^2 is devoid of human habitation and is exclusively available for free ranging lions. In the remaining ∼13,000 km^2 (of which in addition to the National Park another ∼1,600 km^2 are under legal protection as Wildlife Sanctuaries) humans and lions coexist at varying levels of population densities, tolerance toward each other, and magnitude of conflict. Concurrent with a 19.2% rate of human population growth (Human Census Report, Government of India available at www.census2011.co.in) in Gujarat, lions outside PAs (National Park and Wildlife Sanctuaries) have grown by 126% in the last two decades. Consequently, ∼30% of the present lion population resides outside the PAs in close proximity to humans (Gujarat Forest Department, 2015; Singh, 2017a).

The exclusive occurrence of Asiatic lions in the small region of the Gir-Saurashtra landscape has created opportunity for lion tourism which is utilized formally by the local government while illegally by local communities for economic gains. These attributes have been exploited by bureaucrats, politicians and local communities to gain mileage and economic privileges, often at the cost of the long-term conservation interests of Asiatic lions.

Gir lions have been a key subject of management and research; managed as a prized trophy prior to late 1800's (Moose, 1957; Divyabhanusinh, 2005) and subsequently conserved as a symbol of regional and national pride (Rangarajan, 2001). Scientific research on this sub-species commenced in the late 1960's with Joslin (1973) and Berwick (1974). It still continues in the form of the longest ecological research project in India under the auspices of the Wildlife Institute of India between 1986 and 2018 (Chellam, 1993; Jhala et al., 1999, 2004, 2011, 2014a, 2016, 2018). Independent researchers have also addressed certain aspects of lion ecology and conservation such as diet (Sinha, 1987), lion recolonization outside the Gir PA (Dharaiya, 2001), and human-lion interface (Meena et al., 2014). Furthermore, many wildlife management- and monitoring- practices that have evolved in Gir (such as pugmark counts; Wynter-Blyth, 1949) were later adopted across India for tigers *P. tigris tigris* (Choudhury, 1970; Panwar, 1979).

Thus, a unique blend of culture, religion and historical legacy mixes with the science of lion ecology, often being at odds with economics of modernization to create a scenario that necessitates a multidisciplinary approach for conserving the last Asiatic lions. In this paper we review relevant topics related to lion- history, origin, culture, ecology (morphology, demography, behavior, movement, and foraging), conflict, economics, and politics. Our long-term intimate association with the Gir ecosystem provided us with access to information and a better understanding for its interpretation. Information available as reports, guidelines, management plans (that have no Internet access) were systematically reviewed from repositories at the Wildlife Institute of India and the Gir Research Center along with relevant published literature. We evaluate policy and management strategies that have resulted in this conservation success, assess gaps that need to be addressed and highlight impending issues that would need major paradigm shifts for long term survival of these lions.

ORIGIN, HISTORY, AND CULTURE

The work of geneticists, archeologists, and historians have contributed to our understanding of the origin and timing of lions' colonization of the Indian subcontinent. Evidence from the three disciplines do not always corroborate each other and there is still a lot to learn about when and how lions came into India. Two subspecies of extant lions, namely all lions from Africa as *P. l. leo* and lions from Asia as *P. l. persica* were recognized (Bauer et al., 2016). These were believed to have diverged sometime between 55,000 and 200,000 BP (O'Brien et al., 1987). Recent investigations on phylogeography of modern lions, based on mitochondrial and nuclear DNA analysis, indicates a single African origin of modern lions (Barnett et al., 2006; Antunes et al., 2008). Extant lions originated from several Pleistocene *refugia* (324,000–169,000 BP) in East and South Africa (Antunes et al., 2008). Asiatic lions are believed to have originated from an older East African refuge dispersal event some 118,000 BP (95% CI 28,000–208,000 BP) (Antunes et al., 2008). Based on Northern, Western and Central African lions' close genetic proximity to extant Indian lions as compared to Southern and East African lions, Bertola et al. (2011) postulated an alternative explanation, wherein after a Pleistocene extinction event in Western and Central Africa, recolonization occurred from a *refugia* in the Middle East. More recent analysis of mt-DNA from modern and ancient lion samples (Barnett et al., 2014) shows that lion exodus into Asia started as late as 21,000 BP and probably continued till the late Holocene. Maternal lineage of Gir lions was found to be nested within the clade formed by Northern, Western, and Central African lions (Barnett et al., 2014). Bertola et al. (2015) included nuclear markers along with mt-DNA and found lions from India to form a distinct cluster with little/no admixture with African lions. The IUCN Cat Specialist Group now recognizes two subspecies *P. leo leo* consisting of lions from India, Central and West Africa and *P. leo melanochaita* comprised of lions from Eastern and Southern Africa (Kitchener et al., 2017). Fossil records in Sri Lanka (Manamendra-Arachchi et al., 2005) report lion and tiger presence as early as the late quaternary, much before the current estimated arrival of both modern lions and tigers into India. The last land bridge between India and Sri Lanka submerged 5,000–10,000 BP (Yokoyama et al., 2000). Climate and associated vegetation changes are considered as the drivers of extinction of lions, and coupled with hunting by early humans in more recent times arguably caused the extinction of tigers as well in Sri Lanka (Manamendra-Arachchi et al., 2005). However, the possibility of their continued existence in *refugia* on mainland India prior and during the last glacial maxima cannot be ruled out. Though evidence for such claims are yet to be discovered, such possibilities seem realistic and open up a range of questions that are yet to be answered.

The presence of Neolithic/Chalcolithic cave paintings of lions in Bhimbetka rock shelters of central India (30,000–100,000 BP; Badam and Sathe, 1991) suggest lions to be early entrants into India and lend support to the fossil records from Sri Lanka. But their absence at the peak of the Indus valley civilizations as evidenced from the lack of their appearance in seals, pottery, and terracotta images that abound with representations of other contemporary wildlife like tigers, elephants, and rhinoceros (Divyabhanusinh, 2005) remains a mystery. It is possible that the earlier entrant lions became locally extinct within most/all of India as had happened in Sri Lanka. Lion terracotta art was recovered at Mehrgarh near Bolan Pass (currently in Pakistan), one of the important Neolithic (9,000–4,500 BP) archaeological sites and a lion handle was excavated from Taxila (currently in Pakistan) that dated back to late Harappan period (2,500 BP) (Divyabhanusinh, 2005). While depictions of tigers in Harappan art are widely known, a rare find of a two-headed lion like figurine was also recovered from the Indus valley site (Iyer, 1977). The advent of the Aryans and their influence was marked with an increase in the familiarity with lions. It would be difficult to differentiate if this familiarity was because of lions living in India or by Aryans encountering them in Persia during their migration. Ancient Hindu literature, the *Rigveda*, which is dated between 3,500 and 4,000 BP mentions the word *simha* (Sanskrit for lion) at least on 15 different occasions. Based on recorded history, Singh (2007) speculates that modern lions entered India through the western passes of the Hindu Kush and occupied most of Northern and Western India between 2,600 and 3,500 BP. Divyabhanusinh (2005) attributes the entry of modern lions in the Western and North-Western parts of India to the loss of tropical forests caused by environmental changes such as prolonged drought (which is also attributed as a cause for the Aryan migration) and habitat modifications caused by anthropogenic factors like clearing of forests for grazing lands and agriculture. About 3,500 BP the tiger seems to have lost its supremacy to the lion, which was prominently depicted in Indian art, culture, sculpture and literature (Iyer, 1977). Subsequently, by the time Jainism and Buddhism evolved, lions were well-established in India. Contemporaneous ancient Jain and Buddhist literature depicted the lion as a symbol of the 24th Jain *tirthankar* (spiritual leader) Mahaveer (∼2,600 BP); while Gautam Buddha, the son of the Sakya chieftain (born around 2,500 BP) was known as *Sakyasimha* after achieving enlightenment. Lion capital at Vaishali during pre-Mauryan era (2,100–2,300 BP) symbolized the supreme iconic status of the species as a royal symbol. Lions featured in the ancient Buddhist texts of the Jatakas (∼2,400 BP) that depict Buddha as various animal incarnations, often as a noble lion (Choskyi, 1988). The lion was ubiquitous as a symbol of royalty and was given a place of pride in lore and text in Sankrit, Tamil, Pali, and Persian. By the time of the *Puranas* (∼1,000–1,500 BP) and the great epics of the *Ramayana* and *Mahabharata,* the lion became the *vahana* (carrier) of Goddess Durga and was considered an incarnation of God Vishnu as "Narasimha"; and thus became a symbol of worship in Hinduism. In modern Republic India the lion was designated as the national animal (Rangarajan, 2013), a status it subsequently lost to the tiger in 1973 (Rangarajan, 2001). Independent India is often depicted as *Bharatmata* (mother India) riding a full maned lion (Newell, 2011). The 3rd century BCE Ashoka pillar depicting four lions standing back-to-back, within a Persepolitan style proclaiming the ruler's universal all-encompassing vision of *dhamma* has now become the national emblem for India and is printed on its currency and official documents. The recent icon adopted by the Indian Government for encouraging local entrepreneurship is a "make-in-India" logo of an Asiatic lion made from mechanized parts.

MORPHOLOGY

Asiatic lions can often be morphologically differentiated from African lions based on (**a**) skull characteristics, wherein the Asiatic lions have an extra infraorbital foramen, (**b**) a typical loose fold of skin on the abdomen known as the belly-fold which is absent in African lions (O'Brien, 2003), **(c)** facial characteristics of Asiatic lions, with a more elongated snout and a more sloping forehead; giving them a longer profile in lateral view in comparison to the African lions and, (**d**) males having sparser manes, never covering their ears The mane in the adult lion has the typical "mohawk" style look. (**Figure 1**, **Supplementary Material S1**). As part of our long-term research project, we combined our field observations of known lions with techniques developed for African lions to develop criteria for estimating the age of individuals (**Supplementary Material S2**), which helped us construct their population structure and demographic details.

Between 2001 and 2018, we captured 35 free-ranging lions (including sub-adults that were targeted for understanding dispersal) from different parts of the Gir landscape in order to deploy radio-transmitters or for treatments, and recorded their morphometric details. We found average weights of adult males ($n = 7$) and females ($n = 12$) to be 160 (SE 4.7) kg and 116.5 (SE 3.7) kg, respectively (**Table 1**).

Like tigers and leopards, several local variations in lions based on their mane size and coloration, and coat texture have been recorded from different parts of India and from within Gir (Divyabhanusinh, 2005). Adult male lions are often grouped by local communities into various categories based on the color of their manes that can range from golden yellow (*Pinglo*), speckled gray (*Bhurio*) to black (*Kamho*) (Divyabhanusinh, 2005).

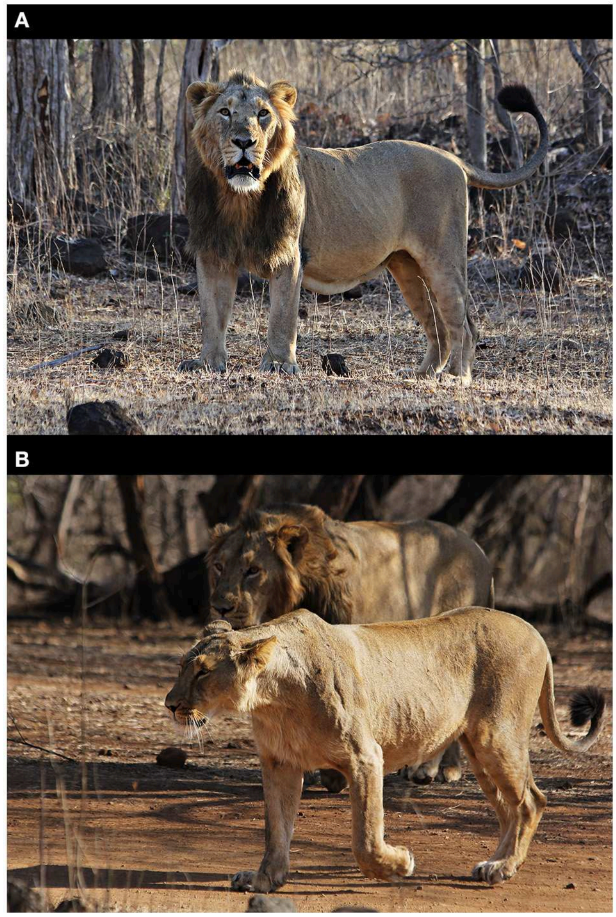

FIGURE 1 | Face and body profiles of Asiatic lions. **(A)** Adult male, note the sparser mane (than African lions) that does not cover the ear and the top of the head with a Mohawk look, and the prominent belly-fold; and **(B)** adult female, with a longer sloping snout and side face profile than African lionesses. Also, note the size difference between the male and the female (a consorting pair). Photographs taken by Stotra Chakrabarti.

Distribution and Status

The erstwhile range of the modern Asiatic lion, reconstructed mainly from paleontological evidence, literature, art, culture, and *shikar* (hunting) documents suggest an extensive area from Anatolia, Syria across the Middle East to Eastern India (Kinnear, 1920; Caldwell, 1938; Joslin, 1973). Till the mid-1800s, lions in India inhabited the entire northern Indo-Gangetic Basin in North and Central India and were abundant in the modern states of northern and western India, Bihar and Odisha in the east with the river Narmada being the southernmost boundary (Fenton, 1908; Pocock, 1930; Dalvi, 1969). Subsequently by late 1800's they were exterminated from most of their range because of hunting and habitat loss (Divyabhanusinh, 2005). By 1880s lions were restricted as a single free-ranging population in and around the Barda and Alech hills, Mitiyala, Girnar, and Gir forests in the Saurashtra peninsula of Gujarat (Dalvi, 1969). Although some lions continued to survive in isolated habitat pockets of Iran and Iraq, but these were not viable populations and soon became extinct. By 1888–1890, hunting and loss of forests due to agricultural expansion and livestock grazing in Saurashtra restricted the lions to a single population in the Gir forests, a patch of about 2,000 km^2 composed of dry deciduous and thorn forest (Divyabhanusinh, 2005).

TABLE 1 | Morphometric details of adult Asiatic lions (n = 19; 12F, 7 M) captured between 2001 and 2018 for deploying radio-collars. Body length is measured from nose-tip to tail-tip along the curves.

Lion ID	Age class	Weight (kg)	Shoulder height (cm)	Body length (cm)	Chest girth (cm)	Tail length (cm)
F1	Adult female	120	96	262	99	85
F2	Adult female	100	103	251	101	88
F3	Adult female	110	81	289	105	80
F4	Adult female	101	89	235	96	64
F5	Adult female	123	94	254	105	78
F6	Adult female	123	93	263	104	84
F7	Adult female	110	98	243	98	66
F8	Adult female	138	98	264	109	83
F9	Adult female	130	-	-	-	-
F10	Adult female	126	97	231.4	106	70
F11	Adult female	97.3	95	241	94	73
F12	Adult female	120	95	241	100	
	Mean	**116.5**	**94.5**	**252.2**	**101.5**	**77.1**
	SE	**3.7**	**1.6**	**4.8**	**1.3**	**2.4**
M1	Adult male	143	97	274	107	81
M2	Adult male	176	98	278	116	90
M3	Adult male	170	104	289	118	88
M4	Adult male	160	110	286	114	90
M5	Adult male	145	103	290	98	90
M6	Adult male	160	99	288.5	110	84.5
M7	Adult male	167	99	288	116	94
	Mean	**160.1**	**101.4**	**284.8**	**111.3**	**88.2**
	SE	**4.7**	**1.7**	**2.4**	**2.6**	**1.6**

Driscoll et al. (2002) suggests that about 2,680 (range 1,081–4,279) BP, the Kathiawar Peninsula that contained the Gir forests was separated from mainland India by rising sea levels in the Gulf of Khambhat (Gupta, 1972), causing the first genetic bottleneck that isolated the founders of the present Asiatic lion population, compelling them to inbreed for several generations (O'Brien, 2003). By the time the Gulf water receded and the peninsula became continuous with the mainland, most of the lions from mainland India had become locally extinct providing little chance to the inbred population to enhance their genetic diversity. A second, less-severe but more popularly known bottleneck occurred at the onset of the 19^{th} century when owing to rampant hunting, Gir lions dwindled to around <50 individuals (Edwardes and Fraser, 1907; Kinnear, 1920; Pocock, 1930).

Owing to the timely protection measures taken by the *Nawab*s of Junagadh who ruled most of the Gir region, lions survived (Divyabhanusinh, 2005) and increased to about 287 by 1936 (Dalvi, 1969). Subsequently, the Government of Independent India enforced a complete ban on lion hunting in 1955 and declared the Gir forests as a Wildlife Sanctuary in 1965. Ensuing protection and habitat management by the Gujarat Forest Department resulted in the lion population increasing steadily (Singh and Kamboj, 1996) to over 500 in the last 2015 total count (Gujarat Forest Department, 2015). The sub-species was also down-listed from the "Critically Endangered" category of the IUCN Red list in 1990s (Nowell and Jackson, 1996) to "Endangered" in 2008 (Breitenmoser et al., 2008).Within the past two decades, lions have dispersed into about 13,000 km^2 of agro-pastoral landscape comprising of the Gir Protected Area (Gir PA; 1700 km^2), Girnar Wildlife Sanctuary (180 km^2) and over 11,000 km^2 of human-dominated landscape and coastal scrublands of the surrounding districts of Junagadh, Amreli, Gir Somnath, and Bhavnagar (Ranjitsinh, 2016; Singh, 2017a). Currently, the Saurashtra landscape has a single source population of lions comprised of ∼300 adult individuals that live within the Gir National Park and Wildlife Sanctuary, and several patchily distributed small sink populations (Pulliam, 1988) of <50 individuals each in the human dominated agro-pastoral system (**Figure 2**). Though these small populations do breed and recruit lions, immigrants from the Gir PA are an essential element for their long-term viability (Banerjee et al., 2010). Radio telemetry (Jhala et al., 2014a) has shown extensive movement between these small populations and with the lion population of Gir PA. Lions thus exist in a classical metapopulation framework in the Saurashtra landscape (Hanski and Gilpin, 1997; Cronin, 2003). Consequently, habitat connectivity that facilitates lion movement between populations is vital for long-term lion persistence in the Saurashtra landscape (Banerjee et al., 2010; Banerjee, 2012).

While the recovery of Gir lions elucidates a conservation success story; it also poses serious challenges for wildlife managers and conservationists in terms of maintaining the future persistence of this subspecies. A population gains security with increasing size and the species becomes secure with increasing number of viable populations (Soulé and Simberloff, 1986). The importance of human free space for large carnivore conservation is undebatable, as conflict with human interests has been the major cause of large carnivore declines worldwide (Woodroffe, 2000). Indeed, lions were often poisoned on livestock carcasses in Gir until recently, when law enforcement became very strict. Currently only 259 km^2 of inviolate space (devoid of human habitation and use) is allocated as Gir National Park for lion conservation in Gujarat. The rest of the protected areas are in the form of wildlife sanctuaries (WLS), reserve forests and protected forests with varying levels of human habitation and legally permitted human use of forest resources (Wildlife Protection Act, 1972), including livestock grazing rights of local semi-nomadic pastoral communities, the *Maldharis*. With land ownership being primarily private in the landscape outside the PAs, creation of new PAs in Saurashtra is difficult. Since the PAs in the landscape have reached carrying capacity for lions with about 300 individuals (Singh, 1997), maintaining the current population of 500 lions or increasing it can only be achieved by ensuring the continued source value of the Gir PA and by providing dispersal corridors to the several small sink-populations in the agro-pastoral landscape. Coexistence with humans thus becomes an inevitable strategy for maintaining a viable lion population in this landscape. However, the Saurashtra landscape is rapidly transforming due to development of linear infrastructure, expanding urban sprawl, agricultural intensification and changing community

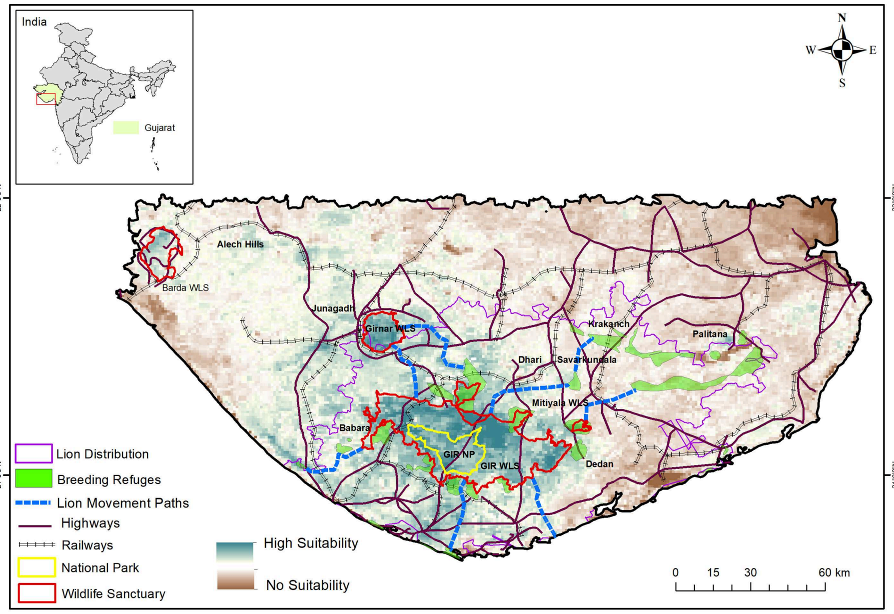

FIGURE 2 | Lion habitat suitability and current lion distribution across Saurashtra landscape overlaid with Protected Areas, breeding refuges outside the protected areas, important lion movement pathways, and linear infrastructure (major roads and railways). Note the location of Barda WLS that is being considered for lion reintroduction.

values. With increasing lion density in this progressively hostile landscape, a multidisciplinary understanding of lion ecology, conflict resolution, and socio-economic underpinnings is required for maintaining lion-human coexistence.

Demography

The earliest attempt to estimate lion population based on *shikar* records were made by William Rice of the Indian Army in 1850s when he concluded that not more than 300 individuals were left in India (Divyabhanusinh, 2005). Subsequent estimates made by forest and army officials under the rule of Junagadh State figured about 20–50 lions in between 1905 and 1913. The first lion census based on pugmark counts at waterholes was conducted in 1936 and reported a total of 287 lions (Wynter-Blyth, 1949). Since 1963, the Gujarat Forest Department has estimated lion numbers about every 5 years by a labor intensive, 3-day total count using livestock bait (Singh, 2017b). In this method, a daily record was kept of all lions that visited the baits. Lions feeding on baits remained localized in the vicinity for 3–4 days. If, however, lions moved away to another bait site a record of the movement was kept and accounted for to minimize double counts while computing total number of lions. The maximum number of lions recorded on any single day was considered to be the total population.

Both pugmark census and total counts depend on unrealistic assumptions, are error prone as they do not address detection issues, require careful identification of duplications, trained field staff and are resource intensive (Williams et al., 2002). To circumvent these issues, we designed and demonstrated lion abundance estimation in a mark-recapture framework (both conventional and spatially explicit) based on individual identification of lions from their vibrissae patterns, ear notches and permanent body marks (Jhala et al., 1999, 2004; Jhala, 2004; Banerjee and Jhala, 2012). Lions >1.5 years were approached within 10–20 m on foot or from vehicles and photographed. Individual lion details (age, gender, identifying features, associated lions, geographic coordinates, photographs, etc.) were then entered in program LION (Jhala et al., 2005) (**Supplementary Material S3**) for storing, archiving, identifying and comparing with the lion database so as to generate information useful for abundance estimation and long-term monitoring of demographic parameters and movement patterns.

Lion density was found to be the highest in the Gir PA at 15 (SE 0.1) lions/100 km^2 followed by Girnar WLS [6 (SE 0.7) lions/100 km^2] and the human dominated landscape of Saurashtra [2 (SE 0.1) lions/100 km^2] (Jhala et al., 2004; Banerjee, 2012; Banerjee et al., 2013). Spatially explicit density of lions in the western part of the Gir PA was positively correlated with tourism hotspots due to artificial food provisioning at these sites (Gogoi, 2015). Due to vegetarian lifestyles of local communities, dead livestock are dumped outside settlements. These carcasses attract large carnivores including lions and leopards (*Panthera pardus*). To minimize encounters between large carnivores and humans as well as to enhance sighting of lions by tourists, wildlife managers often retrieve such livestock carcasses from forest settlements and dump them at tourist viewing spots. This assured food source increased pride sizes and reduced their home ranges (Gogoi, 2015; Jhala et al., 2016). This distribution pattern caused by subsidized food resources overrides the influence of natural prey and other ecological factors, resulting in local lion densities that are higher than natural densities. We believe that though this practice would enhance tourist viewing but will have serious implications on the social organization of lions, spread of infectious diseases and might cause enhanced predation pressure on wild prey in small pockets harboring artificially enhanced lion density.

Allozyme and microsatellite studies indicate that the Asiatic lions have low genetic diversity due to an isolated, inbred population with a small founder base (Wildt et al., 1987; O'Brien, 2003). However, random amplified polymorphic DNA analysis showed some levels of polymorphism in Asiatic lions (Shankaranarayanan et al., 1997). O'Brien et al. (1987) and Wildt et al. (1987) found that Asiatic lions and cheetahs showed a high incidence of morphologically abnormal spermatozoa (79 and 71%, respectively) when compared to free-ranging African lions (25–61%) and other species such as bulls *Bos spp.* and dogs *Canis lupus familiaris* (20–30%). The serum testosterone (a critical hormone for spermatogenesis) was low and Asiatic lions had lower variability in the major histocompatibility complex gene responsible for immunity (Wildt et al., 1987). Todd (1965) attributed dentition abnormalities in Asiatic lions to inbreeding. Decreased heterozygosity likely diminishes reproductive vigor and long-term survival of a population (O'Brien et al., 1986; Packer et al., 1991).

In order to understand the demographic parameters of Gir lions, 68 adult lions, and 91 cubs from 38 litters were intensively monitored using telemetry and individual lion ID profiles (Banerjee and Jhala, 2012). Records of opportunistic mortality events ($n = 228$) were used to understand mortality causes. Gir lions apparently increased from about 177 in 1968 to about 523 by 2015 with an $r = 0.022$ (SE 0.001) translated into an annual population growth of 2.2%. Male: female ratio was 0.63 (SE 0.04) while cub: adult lioness ratio was 0.37 (SE 0.02). Though breeding is observed year round, mating peaked in winter while birth peaked in late summer. Average litter size was 2.39 (SE 0.12). Inter-birth interval was 1.37 (SE 0.25) years ($n = 7$ lionesses) and was higher [2.25 (SE 0.41) years] when cubs of the previous litter survived to independence. Cub (<1 year) survival was 0.57 (SE 0.04) while survival from cub to recruitment age (3 years) was 51% (SE 4%) with infanticide attributing to 30% (SE 7 %) of mortalities. Average annual survival rate of adult lions (>3 years) was 0.9 (SE 0.12). Based on records of 228 lion mortalities recorded between 2007 and 2019, we estimated that 30% of the deaths were caused by diseases (**Figure 3**). Adult lions died primarily due to natural causes (60%), however, human caused mortality was also substantial (32%). Deaths due to falling in open irrigation wells, electrocution by live wires deployed illegally to prevent crop damage from nilgai (*Boselaphus tragocamelus*) and wild pigs (*Sus scrofa*) were a cause of concern in the agro-pastoral landscape. These are being addressed by wildlife authorities by subsidizing the construction of parapets around open wells and pulsating solar-powered wildlife fences to agricultural fields.

Banerjee and Jhala (2012) had concluded that demographic parameters of Asiatic lions did not differ from those of African lions, and went on to suggest that there was no evidence of inbreeding depression on vital rates. Subsequently, there have been recorded instances where free-ranging lion cubs were detected with missing and malformed limbs, or were born blind (**Supplementary Material S4**). These are potential indicators of inbreeding (O'Brien, 1990), and in nature such handicapped individuals rarely survive to propagate these traits, thereby purging out deleterious alleles from the population over time (Keller and Waller, 2002). Intensive health care of wild lions as practiced in recent times by wildlife managers (between 2001 and 2010, 501 lions were captured and treated by Gujarat Forest Department, Pathak et al., 2002; Meena and Kumar, 2012) ensures survival of many such unfit individuals. Such tampering with natural selection processes can have serious implications on the future survival of wild lions (Banerjee and Jhala, 2012).

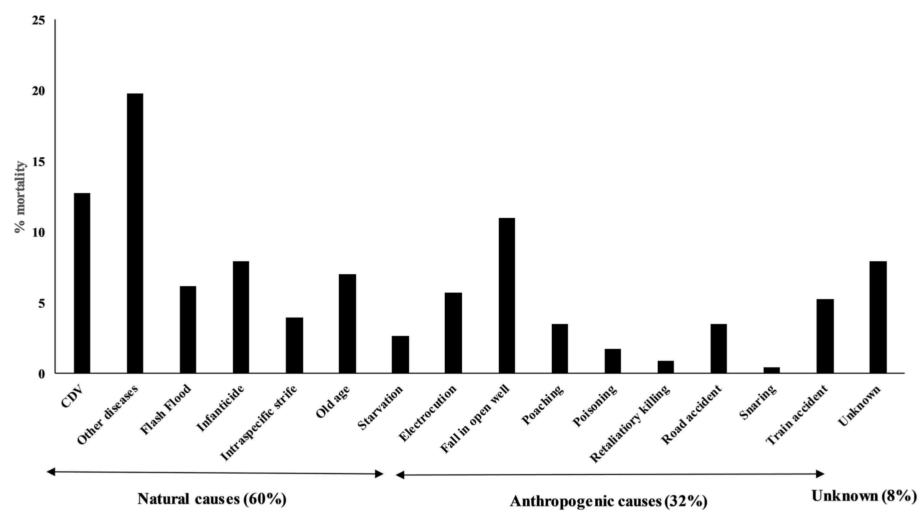

FIGURE 3 | Causes of mortality among free-ranging Asiatic lions ($n = 288$). Lions primarily died because of natural causes (60%), while anthropogenic reasons for mortalities (32%) were substantial. Among the natural deaths, 33% were due to canine distemper virus and other diseases.

Social Organization and Behavior

Though biologists have been observing lions in Gir since 1960's (Joslin, 1973), quantitative data on lion social behavior has only just begun to accumulate (Chakrabarti and Jhala, 2017, 2019). In free-ranging Asiatic lions, prides comprise only of females and their dependent cubs, while adult males (singletons or coalitions) form separate units covering the ranges of multiple female prides (Joslin, 1973; Chellam, 1993). However, adjacent female prides were found to have exclusive territories and such territories remained almost constant over the years (Chakrabarti and Jhala, 2019). Females of a pride rear cubs together in a crèche, but estrus synchrony is not as prominent as reported in their Serengeti counterparts (Chakrabarti and Jhala, 2017). Cubs are weaned at 5–6 months of age but remain dependent on their natal pride for food till 2–3 years of age (Joslin, 1973; Banerjee and Jhala, 2012).

Unlike as reported for egalitarian African lion societies (Packer et al., 1988), Asiatic male lions form hierarchical coalitions wherein every coalition has one dominant male who appropriates >70% of all matings and 45% more food from his subordinates from shared kills (Chakrabarti and Jhala, 2017). Owing to such strict linearism in resource appropriation between male partners in the Asiatic lion coalitions, males belonging to coalitions of two acquired higher benefits compared to single and low-ranking males in large coalitions (of >2 males). This has resulted in an optimum coalition size of two males in the Asiatic system (Chakrabarti and Jhala, 2017).

Interactions between the two sexes are limited primarily to mating and occasionally on large kills (Meena, 2008; Chakrabarti and Jhala, 2017). Male lions frequently fend for themselves: hunting on their own, scavenging livestock carcasses and kleptoprasitizing kills made by leopards and lionesses (Chellam, 1993; Meena, 2008; Banerjee et al., 2013). Asiatic lions thus form same-sex groups, where each group behaves more like a solitary carnivore and act as independent entities (Chakrabarti and Jhala, 2019). Group sizes are smaller in the Asiatic system with male and female groups averaging at 1.7 (SE 0.2) and 2.5 (SE 0.4) adults, respectively (Gogoi, 2015). Such operational and functional separation between females and males seem to be in contrast with lion societies reported from the Serengeti and Ngorongoro (Schaller, 1972; Bertram, 1978; Packer et al., 1988). However, degrees of male-female interactions akin to that found in Gir have also been reported from lions in the Luangwa valley in Zambia, where hunting of males have severely reduced their numbers and hence, ability to maintain exclusive and all-round access to female groups (Yamazaki, 1996).

Male coalitions (with ≥2 male partners, $n = 7$) had an average home range (95% Minimum Convex Polygon) of 120 (SE 19) km^2, much larger than single males ($n = 4$) averaging at 31 (SE 3) km^2. Single males had shorter tenures as territorial breeders [14 (SE 3) months) than coalition males [30 (SE 4) months] (Chakrabarti and Jhala, 2019). For reproducing successfully, a male needs to hold tenure for over 24 months so as ensure that cubs sired by him reach recruitment age and are not killed by infanticidal new territorial males (Schaller, 1972). In cases where resident male(s) were ousted by new male(s), cubs and juveniles <18 months of age were mostly killed by the new males or rarely survived when forced to disperse (Chakrabarti and Jhala, 2019).

Chakrabarti and Jhala (2019) hypothesizes that this disparity in group size and male-female association from the lions in the Serengeti can be attributed to plasticity of social behavior in response to the differences in resource availability between the two systems. Asiatic lions subsist on smaller prey (modal prey- chital *Axis axis*, averaging at around 45 kg) (Meena et al., 2011; Banerjee et al., 2013; Chakrabarti et al., 2016), resulting in heightened intra-group competition for food and ensuing smaller group sizes (Chakrabarti and Jhala, 2017). Furthermore, in the Asiatic system prey species are non-migratory and evenly distributed at reasonably high densities; resulting in smaller and seasonally uniform female pride territories (Jhala et al., 2009) and higher lion density. This possibly allows males to maximize their reproductive potential by encompassing many female prides within their home ranges simultaneously. These arguments pertaining to prey- size and availability are in consonance with circumstances prevailing in West and Central African lion populations, where the lack of large prey has been reported to have resulted in small group sizes in lions (Bauer et al., 2003). Furthermore, it has been reported from the woodlands in Kruger that male lions were often found to be loosely associated with a particular pride of females; and spent more time patrolling territories, hunting on their own and mingling with other female groups (Funston et al., 1998). Such a system somewhat mirrors the degree of male-female association in the Asiatic lion population, and as postulated by Funston et al. (1998), availability of ample cover seems to be one of the driving mechanisms for such a societal regime. With dense cover that aids in concealment, female lions likely require less assistance from their pride males in safeguarding cubs from marauding, infanticidal males (Funston et al., 1998). Following this argument, Chakrabarti and Jhala (2019) opined that dense cover in the deciduous Gir forests may have also prevented male Asiatic lions from controlling the females and retaining exclusive access to a female group.

In the Asiatic system, although male coalitions encompass multiple female groups, none of the female prides remain exclusive to any particular coalition (Meena, 2008; Banerjee, 2012). Such non-exclusivity of female groups to particular males/coalitions have compelled and allowed females to be promiscuous, where lionesses were found to mate with multiple neighboring (rival) coalitions (Chakrabarti and Jhala, 2019). In systems, where male coalitions have mostly exclusive mating rights over pride females (like in the Serengeti), extra coalition paternity are rare (Gilbert et al., 1991). But in land tenure systems where lionesses encounter multiple male coalitions who can potentially kill unfamiliar cubs, promiscuity likely aids females to familiarize with several males and buffer infanticide (Chakrabarti and Jhala, 2019). Furthering this thought, extra-coalition paternity has been reported from lions in Etosha where a genetic assessment has revealed that 41% of the cubs in the population were borne out of multi-male promiscuous matings (Lyke et al., 2013). The social organization and sexual strategies of lions differ across their entire global range of habitats, highlighting resource-mediated and anthropogenically (hunting pressure) driven behavioral plasticity in lions inhabiting diverse eco-regions (Chakrabarti and Jhala, 2019).

Habitat Needs and Activity

We used VHF, GPS, satellite telemetry and long-term monitoring of known individuals to understand ranging patterns, land tenure, habitat use, and activity patterns of lions ($n = 97$) across the Saurashtra landscape. Besides obtaining regular fixes (locations ranging from one per hour to one in 3 days), we followed each radio-collared lion on foot and/or a four-wheel drive vehicle continuously for 192–360 h sessions and carried out an all-behavior sampling [n = ∼6,412 hours of continuous monitoring data from 27 telemetered lions] (details available in Banerjee, 2012; Banerjee et al., 2013; Jhala et al., 2016).

Within the Gir PA, home ranges (95% MCP) of territorial males averaged at 91 (SE 17) km^2; which were more than three times the ranges of breeding females [27 (SE 8) km^2]. Lion home ranges in the human-dominated landscape outside the Gir PA were much larger than those inside the PA [territorial male = 832 (SE 42) km^2; breeding female = 169 (SE 57) km^2]. Core area (50% Fixed Kernel) of breeding lionesses inside Gir PA [7 (SE 3) km^2] were four times smaller than that of breeding lionesses outside the Gir PA [30 (SE 15) km^2] (Banerjee, 2012; Chakrabarti, 2018). Larger home ranges of lions in the outer landscape is in accordance to the Resource Dispersion Hypothesis (Macdonald, 1983) attributable to patchy distribution of resources (prey and suitable habitats) in the landscape, while within the Gir PA these are uniformly available.

Banerjee (2012) found average territorial tenure of males ($n = 7$) to be 36 (range 18–60) months while average age at dispersal from natal prides for sub-adult males ($n = 6$) to be 3.9 (SE 0.13) years. We observed an old displaced male to successfully re-establish another territory and even father cubs after spending some time as a nomad. Average shift between successive territories for adult males was 21 (SE 5) km, while dispersal distance of sub-adult males from their natal territories was 16 (SE 4) km (Banerjee, 2012). Contrary to our expectation, activity patterns of lions within and outside PAs differed very little (**Figure 4**), attributable to the omnipresent human activities in the landscape and within the PAs (tourism, pilgrimage, grazing of livestock, and commercial activities of *Maldhari*s).

Gir vegetation primarily comprised of thorn and deciduous forests along with evergreen riverine patches (Qureshi and Shah, 2004). These riverine patches were critical lion habitats that provided respite from the summer heat (Jhala et al., 2009). Creation of the 259 km^2 National Park in 1975 after removal of 592 *Maldhari* families from central part of the Gir PA and recovery of the forest after the cyclone of 1982 has resulted in an increase in shrub (*Helicteres isora*, *Holarrhena antidysenterica* etc.) and tree density within the Gir PA (Khan, 1993; Sharma, 1995; Basu, 2013). Wildlife managers believe that this increasing vegetation density makes the habitat unsuitable for lions and their prey (Sinha et al., 2004), and have recommended selective thinning (Singh and Kamboj, 1996). However, wild ungulates of Gir are primarily browsers while domestic livestock are grazers (Dave and Jhala, 2011). Therefore, management interventions of opening habitats (besides removal of exotic invasive weeds like *Senna uniflora* and *Lantana camara* that abound in the livestock grazed areas of the PA) should be done only after careful site-specific evaluation.

Within the agro-pastoral landscape outside the PA, core areas of lion home ranges were composed of agriculture and thorn forests (Banerjee, 2012). Home range cores were observed to be farther from villages and townships but were closer to drainage

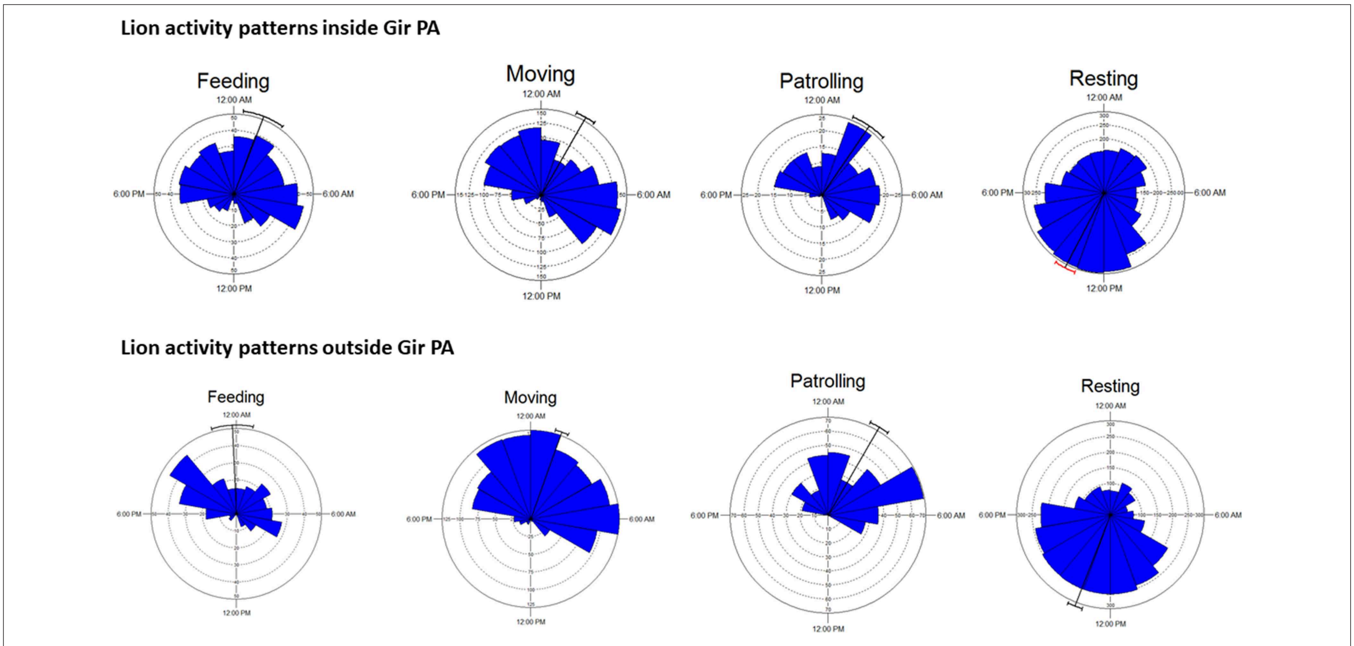

FIGURE 4 | Activity patterns of lions ($n = 27$ radio-collared lions) inside and outside Gir PA based on continuous (day-night) all behavior sampling data (∼6,400 h). Major behavioral states have been depicted.

and PAs (Banerjee, 2012; Jhala et al., 2016). Lions were active at night in this human dominated landscape, often venturing into villages and townships to hunt livestock. However, with advent of human activities during the day, lions sought concealment in vegetation cover. Average day time refuge patch size of lions in the human dominated landscape outside the PA was 7.5 km^2 (SE 0.74) but even small patches of vegetation (5–7 ha) were used. However, successful breeding by lionesses in this landscape required habitat patches of >4 km^2 (Banerjee, 2012). These findings through radio-telemetry highlight the importance of small interspersed vegetation patches characterized by thickets of *Prosopis juliflora* and *Acacia senegal* for lion persistence in the larger agro-pastoral landscape of Saurashtra (**Figure 2**). Remotely sensed time-series data on land cover changes suggests that this agro-pastoral landscape is rapidly being converted into urban setup with increasing development of linear infrastructure (Basu, 2013). Such infrastructure are detrimental for continued lion occupancy of the landscape as they will remove breeding and day-time refuges, as well as hinder dispersal routes between lion populations in the landscape and the PA. If lions are to continue to persist in this landscape, urgent changes in land policy and infrastructure development are required to safeguard these critical habitat patches and their connectivity.

A successful strategy for conserving large carnivores is to maintain a metapopulation structure (Hanski, 1994) within the landscape wherein one to many populations, that are demographically and genetically connected, act as source populations (Chapron et al., 2008; Walston et al., 2010). Preferably the source population habitat(s) for a large carnivore should be inviolate, wherein carnivores can subsist on natural prey and perform their ecological role. For Asiatic lions, such an area is a small National Park (259 km^2), that can at best accommodate 25 lions which are demographically not viable by themselves (Banerjee et al., 2010). For tiger reserves in India, a minimum population of 20 breeding females is considered to be viable (Gopal et al., 2007; Chapron et al., 2008). To achieve this, an area of 800–1,000 km^2 is required, and has been legally mandated to be made inviolate by incentivized voluntary relocation of human settlements from Tiger Reserves to delineate core areas (Gopal et al., 2007). A similar approach is required for Asiatic lions and an additional area of the Gir WLS needs to be legally demarcated and augmented to the existing National Park so as to cover a total of about 800–1,000 km^2. Land ownership outside the PA is predominantly private and the Gujarat Forest Department has little control over changes in land-use patterns. Therefore, after securing a viable lion population within an inviolate space, protected areas under less stringent categories like conservation and community reserves that permit uses by local communities and safeguard their livelihoods [Wildlife (Protection) Act 1972 (2006 amendment)] should be used to conserve habitat patches within the larger human dominated landscape. Currently, radio-telemetry has shown that lions move across the landscape freely using certain land use categories and topographical features like drainage systems (Banerjee, 2012). However, the expansion of existing roads into heavy traffic highways, railways, and other linear infrastructure is likely to severely curtail such movement. Using lion locations from telemetry (>9,000), a habitat suitability map using an ecological niche factor analysis (Hirzel et al., 2002) was prepared and optimal connectivity between lion habitat patches modeled using PATHMATRIX (Basu, 2013; Jhala et al., 2016; **Figure 2**). These habitat corridors are the minimal requirements for lions to move between habitat patches and maintain the landscape scale metapopulation structure. Infrastructure that cuts through lion habitat patches and corridors needs to be made lion friendly and permeable using wildlife under- and over-passes (Jhala et al., 2016). The only legal provision available to regulate land use conversions in such lion habitats is by the provision of declaring Ecosensitive Zones under the Environment Protection Act (1986). Identified habitat patches and corridors (**Figure 2**) should be made part of the ecosensitive zone of the Gir PA. Such a declaration by the Government of Gujarat would enable authorities to reduce further losses of these areas to industry, mining and infrastructure while permitting uses that are conducive to lion conservation and local livelihoods. Currently, the Gujarat Forest Department is primarily responsible for lion conservation across the landscape, a responsibility that needs to be shared with various stakeholder agencies including roadways, railways, electricity, and civil administration. Such a multi-collaborative approach would ensure that development and conservation go hand-in-hand and are not always at loggerheads.

Food Habits and Foraging

Until early 1970s, Gir PA was dotted with about 300 *Maldhari* settlements (*nesses*) having over 40,000 livestock that formed the staple prey of lions (75% of their diet, Joslin, 1973), while wild ungulate numbers in the PA were few (5,600, Berwick, 1974). In 1975, when Gujarat was under the federal Government rule, about 190 *Maldhari* families along with their livestock were resettled outside Gir PA. In 1982 Gir experienced a major cyclone that uprooted ∼2.5 million large trees, resulting in the opening of the canopy and increased browse availability for ungulates (Dave and Jhala, 2011). Reduction in competition from livestock (Khan, 1993; Sharma, 1995) coupled with increased food availability by the cyclone and better law enforcement that checked poaching are believed to have resulted in the recovery of wild prey (Dave and Jhala, 2011). Regular monitoring of prey using line transect based distance sampling compared with data on prey estimates from Joslin (1973) and Berwick (1974) show that wild ungulates increased in their numbers till early 2000, and since then have reached stable densities (Jhala et al., 2016). Consequently, proportion of domestic livestock in lions' diet within the PA declined to 52% by the 1980's (Sinha, 1987) and further to 25% (Chellam, 1993; Meena et al., 2011; Banerjee et al., 2013) during the next three decades.

We investigated lion foraging ecology through direct continuous observations on radio-collared lions to record feeding events (>6,000 h observation on 27 lions), and through scat analysis ($n = 495$). The Saurashtra landscape supports a large livestock population (∼6.4 million, Junagadh Agricultural University, 2016). With majority of the people being vegetarian combined with the religious sentiment of Hinduism and Jainism, cattle are not consumed for meat. Several charitable cattle camps (locally known as *Gaushala*s and *Panjrapole*s) that house old and unproductive cattle are distributed across the landscape. Livestock carcasses are usually dumped at specific locations called *haddakhodis* outside villages and such *Panjrapoles*. Carnivores including wolves (*Canis lupus pallipes*) and striped hyenas (*Hyena hyena hyena*) within agro-pastoral landscapes rely predominantly on this assured food source (Jhala, 2002) across India. This factor has played a major role in promoting and sustaining the dispersal of lions outside of the PA. Lions are opportunistic feeders and rely both on predation and scavenging. Occurrences of food remains in scats are unable to distinguish between predation and scavenging, and if used alone can overestimate livestock-lion conflict. By using both direct observation on feeding events and scat analysis, Chakrabarti et al. (2016) was able to quantify contribution of dead livestock to lion diet. Chakrabarti et al. (2016) further developed models for estimating biomass consumption from prey occurrences in scats by conducting feeding experiments on lions, correcting previous diet estimates from lion scats that were fraught with considerable biases owing to the use of an incompatible model developed by Ackerman et al. (1984) for pumas (*Puma concolor*). Optimal foraging models developed by Chakrabarti et al. (2016) suggest that due to constraints of gut fill, passage time and carcass decomposition; medium-sized prey like chital comprise of the principal prey for large carnivores, including lions, in tropical systems. Lion diet outside the PA was composed of 25% wild prey and 75% livestock (Banerjee, 2012). However, telemetry data demonstrated that among the total consumption of livestock, 35% was from actual predation while 65% from scavenging (Banerjee, 2012). Rarely were prized productive livestock killed by lions due to the husbandry practice of stall feeding and corralling such livestock during the night (Banerjee, 2012). Farmers were tolerant toward lions in their vicinity and property due to lions acting as effective predators for nilgai and wild pigs that caused substantial crop damage in this landscape.

Lion-Human Conflict and Coexistence

The Gir forests have been inhabited by the *Maldhari*s for the past 200 years (Casimir, 2001). *Maldharis* have strong ethics and sentiments toward nature and natural resources. They are primarily vegetarian and their major livelihood is livestock husbandry for sale of dairy products. This religious and social background makes them tolerant toward lions, a powerful figure in their folklore and culture. Yet, *Maldharis* persecute lions to deter them from attacking their stock with sling shots, axes, and staffs. In the past, lions have also been poisoned on livestock kills. The *Nawab* of Junagadh recognized this threat early on and commenced a livestock depredation compensation scheme to the owners of livestock killed by lions. This scheme has been continued by the Gujarat Forest department and is revised regularly to keep pace with livestock market prices (**Supplementary Material S5**). Lions loath *Maldharis* and keep their distance when detected by them and their livestock. The water buffalo (*Bubalus bubalis*), that constitutes the majority of the livestock (78%) kept by *Maldharis*, herd together and defend themselves against lions (Banerjee et al., 2013). The husbandry practices of *Maldharis* are honed over years of experience to minimize losses to predation. Livestock are grazed in forests during the day and corralled in thorn bomas during the night. The herd leaves the boma much after sunrise with one to three herdsmen (depending on the size of the herd) and returns back around sundown. The grazing herd structure is composed of cattle and juvenile male buffalos at the front with prized buffalos in the middle, and herdsmen at leading and trailing ends. During lion attacks, the cattle and juvenile livestock (least expensive) scamper and run, becoming most vulnerable. Adult buffalos form a protective ring, often attacking lions in this formation under directions of the herdsmen, and rarely get killed (Banerjee et al., 2013). Dead livestock of *Maldharis* are dumped at specific sites and lions use this resource extensively. Radio-collared lions within the PA were observed to make regular excursions to these dump-sites near the *nesses* in search of free food (Jhala et al., 2016). Therefore, lions do benefit from *Maldhari* livestock through scavenging opportunities and occasional predation, only when strict law enforcement along with a fair livestock depredation compensation scheme control for lethal retaliation against them. The *Maldharis* that live in lion habitats benefit from getting free access to forest resources for themselves and their livestock. We found that *Maldharis* living within the Gir forests made 76 (SE 0.05) % more profits than livestock herders living outside the Gir forests (Banerjee et al., 2013). Thus, the relation between *Maldharis* and lions is far from harmonious coexistence, it is more of co-occurrence with benefits to both parties that are maintained by a delicate balance through cultural attitudes, strict law enforcement, fair compensation scheme for livestock kills, livelihood benefits to *Maldhari*s and rare attacks on humans by lions. A total 190 lion attacks on humans have been recorded between 2007 and 2016 in the Gir landscape, of which a small proportion ($n = 12$, 4%; 1.3 attacks/year) resulted in human fatalities. While attacks by leopards on humans in the same landscape were 383 between 2011 and 2016, out of which 41 were lethal (∼7/year). Elephants (*Elephas maximus*) and tigers cause higher losses to human lives (408 and 34 human deaths/year respectively between 2013 and 2015) across India (answer to *un-starred* question no. 2581, The Lok Sabha, Government of India, 2017; accessible at http://www.indiaenvironmentportal.org.in/files/file/Human-Wildlife%20Conflict_0.pdf). Attacks on humans by lions were observed to increase during years of extreme droughts that caused large livestock populations to enter and graze within PAs (Saberwal et al., 1994). Data from telemetered lions show that lions were mostly non-hostile to humans (one in ten thousand encounters translated into an attack, Jhala et al., 2016). Attacks were mostly accidental: lions rarely stalked or targeted humans as prey, but usually attacked in self-defense or when spooked (Banerjee, 2012).

Livestock densities within a PA beyond a threshold were detrimental to native vegetation communities and wild ungulates (Dave and Jhala, 2011). Profuse growth of weeds and unpalatable vegetation were found to grow in the vicinity of *ness* sites (Dave, 2008). Lions, on the other hand can do well without livestock in their diet and will adjust their densities to natural levels based on the availability of wild ungulates (Schaller, 1972; Van Orsdol et al., 1985) which are reasonably high in Gir PA (63/km^2; Jhala et al., 2016). Therefore, creating additional inviolate space within the Gir PA by relocating the remaining *nesses* to increase the area

FIGURE 5 | Attitudes of local people ($n = 680$ respondents) from 254 villages in the landscape outside the Gir PA regarding the continued presence of lions in their neighborhood. The respondents were categorized based on their livelihoods. The category "others" primarily represent individuals associated with the tourism industry like hoteliers, safari-vehicle providers, etc.

under the National Park would not only benefit lions but the entire native biota of the region. At the least, *Maldhari ness* sites should be rotated every 4–5 years to allow native vegetation to recover from the heavy grazing and trampling effects of livestock (Dave and Jhala, 2011).

Banerjee (2012) interviewed 680 local residents in the landscape using structured interviews to gain an understanding on their attitudes toward lions. Besides the common factor of culture and religion that helped foster lion presence in the human dominated landscape, factors related to livelihood benefits differed from those that operate inside the PA. Pastoralists, on the contrary, were not tolerant toward lions because of the losses they incur from lion predation on their livestock and occasional attacks on them when they attempted to deter lion predation on their livestock (**Figure 5**). Analysis of last 5-year data on livestock kills by lions across the entire Saurashtra landscape (914 villages) suggests an increasing trend in the intensity of depredation (**Figure 6**). Livestock kills were compensated by the Government, and these helped ameliorate retribution. However, pastoral communities outside the Gir PA were not satisfied with the Government compensation scheme (Banerjee, 2012) since there were no free resources (like for *Maldharis* inside the PA) and there was a significant deficit between the market rate for livestock and compensation paid for lion predation (Jhala et al., 2018). Rarely do compensation schemes take into account the "lost opportunity cost" and therefore even when compensated at market rates, predation does take a toll on livelihoods (Banerjee et al., 2013).

Economic reasons were found to be the most significant factor shaping people's tolerance toward lions in the landscape. Communities making direct or indirect profit from lions were more tolerant toward them (**Figure 5**). The two important economic benefits from lions were: (a) their propensity to predate nilgai and wild pigs, both considered as agricultural pests. With no hunting allowed in India, these ungulates can achieve high densities and cause severe local economic losses to livelihoods, (b) presence of lions offered an opportunity for tourism and employment. The Gir PA has a tourism zone where wildlife enthusiasts can visit for a safari, which has encouraged tourist resorts and correlates to flourish in Western Gir. This has economically benefited the local communities residing in this region of Gir. However, not all tourists get to see lions, and the PA management has imposed several restrictions on limited number of vehicles, on-foot access, baiting of lions, etc. Such restrictions are difficult to enforce on private lands across the 13,000 km^2 of lion occupied Saurashtra landscape. Local communities avail this opportunity and conduct "lion shows" outside the PA (Singh, 2017b). Such shows primarily comprise of lions being attracted on private lands through subsidized food (baits/carcasses), while tourists pay the owners of these farmlands to watch lions in action. The tourists often pay exorbitant amounts for these shows as they are guaranteed sightings of lions and granted liberties with them (night photography, watching lions on foot and/or from close proximity) that can be dangerous for tourists as well as lions. However, the profits from such shows are not shared equitably and monopolized by few powerful members of the community. Though considered "illegal," such lion shows are difficult to control and are a major source of lucrative and easy income for locals across the agro-pastoral landscape. Thus, in our assessment, lion-human coexistence in the human dominated landscape has been possible due to: (a) low lion density (about 2–3 lions per 100 km^2); (b) low levels of conflict, lions subsist by scavenging dead livestock, predate unproductive cattle (that are reasonably compensated), and rarely attack humans. Problem lions are immediately removed by management; (c) economic benefits to local communities through removal of crop pests and revenue generation via lion tourism; (d) high level of tolerance of local communities due to religious and cultural attitudes; and (e) strict laws and their enforcement against killing of lions. Changes in any of these factors can disrupt the current

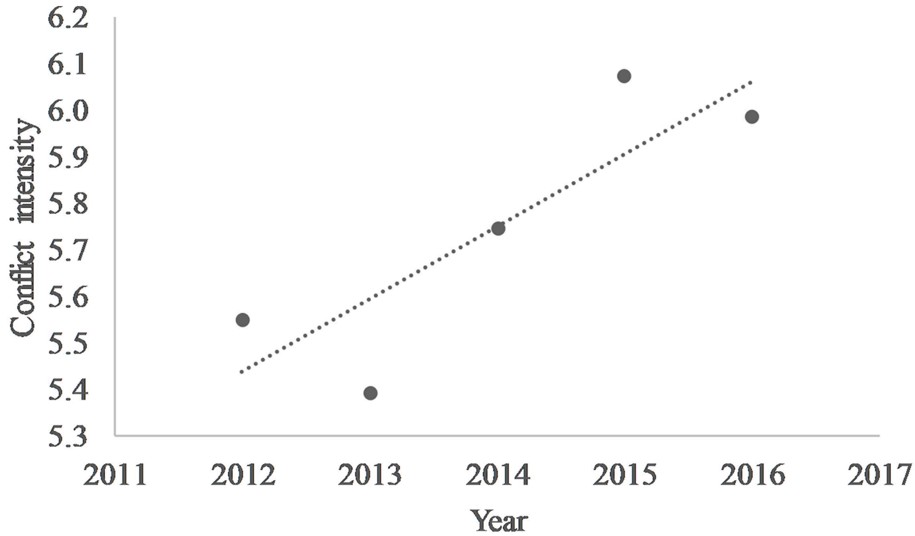

FIGURE 6 | Trend in the intensity of livestock predation (*number of predation events/number of villages with predation*) by lions in between 2012–2016 within the Saurashtra landscape. The data on livestock kill by lions encompasses a total of 914 villages across the entire range of Asiatic lions.

coexistence. However, since lions continue to increase in density and occupancy across Saurashtra, it is a matter of time before they exceed social tolerance limits. There is a perceived shift in the values of local communities from those of tolerance and reverence toward direct economic gains (Banerjee, 2012). Although attacks on humans are rare, the psychological (Löe and Röskaft, 2004) and socio-economic consequences of these attacks can be dire for future lion-human coexistence in Saurashtra.

Also, recently, the wildlife authorities have seriously implemented measures to curb "lion shows" by local communities. This may have serious consequences on continued lion persistence in the human dominated landscape, if indeed this action manages to stop such shows. Communities that cannot have direct profits from having lions in their backyards may not be willing to have them there anymore.

Majority of the people in the agro-pastoral landscape of Saurashtra have a positive attitude toward lions (Banerjee, 2012; Meena et al., 2014). This is vital, but a positive attitude by the majority does not necessarily translate into tolerant coexistence, since it is the behavior of the few but resentful people that ultimately determines the dynamics of human-lion interface (Kansky and Knight, 2014). Such behavior is largely determined by a combination of factors relating to their personal situation and experiences, psychological factors and value judgement (Barr, 2003). Understanding biological and social carrying capacities (threshold for human tolerance) for lions thus becomes important in managing coexistence in this multiple-use landscape of Saurashtra. For example, ranches adjacent to Kenya's Tsavo East National Park, lose 3% of their herd's total economic value to lions; nonetheless, the ranchers are prepared to tolerate a population of ∼26 adult lions whose diet consists of 6% livestock, costing the ranches US$290/lion/year (Patterson et al., 2004). We suggest that lion density outside the Gir PA should be maintained below social carrying capacity and problem lions should be removed immediately from the vicinity of the people. Guidelines for such removals can be adopted from the Standard Operating Procedures developed for tigers and leopards in India (National Tiger Conservation Authority, 2013), keeping in mind the social dynamics of lions (Whitman et al., 2004). Thus, a futuristic and multifaceted policy is required to permit this delicate balance of human-lion coexistence to continue.

A Second Home for Lions and the Mist of Conservation Politics

A single population of an endangered species is susceptible to extinction events caused by environmental and demographic stochasticity (Soulé, 1987). The 1994 outbreak of canine distemper virus (CDV) in the Serengeti killed an estimated 33% of the lion population (Roelke-Parker et al., 1996). An epidemic of such magnitude in Gir could potentially put the Asiatic lion at a high risk of extinction. Gir lions have tested positive for CDV, feline parvovirus, feline herpesvirus, feline immunodeficiency virus and peste des petits ruminants virus (Sabapara, 2002; Ramanathan et al., 2007; Balamurugan et al., 2012). Lions move regularly between habitat patches in the landscape and share space with feral dogs, cats, and other carnivores, creating a condition for the spread of epidemics. A recent infection of canine distemper virus killed a minimum of 28 lions in 2018 as per official records in the eastern part of the PA. However, the actual death toll could be of epidemic proportions, but remains unknown, since many carcasses remain undetected in the wild and investigations were limited only to park authorities.

The threat of extinction due to disease and natural calamities to this single population of lions was recognized early on by the Executive Committee of the Indian Board of Wildlife during a meeting held in Gir in 1956. The first attempt to establish a second population in Chandraprabha in the state of Uttar

Pradesh was undertaken in 1957 (Negi, 1969). Though these reintroduced lions initially bred and increased to 11 individuals from the founding population of five, they were subsequently poached out by 1965 (Negi, 1969). After initiation of modern scientific studies on Asiatic lions, Joslin (1985) and Sale (1986) emphasized the need for establishing a second population away from Gir. This was followed by a population-habitat viability analysis workshop in 1993, wherein all stakeholders, including the Government of Gujarat agreed to the need of establishing a second lion population as an insurance against extinction (Ashraf et al., 1995). The Wildlife Institute of India was mandated with the task of identifying a site for establishing this insurance population. From the three potential sites surveyed (Sitamata, Darrah-Jawaharsagar, and Kuno) within the recent historical range of the lion, the area of Kuno Wildlife Sanctuary (345 km^2) in the central Indian state of Madhya Pradesh was found most suitable since it was located within an intact forested landscape of about 3,300 km^2 (Chellam et al., 1995).

Substantial efforts were made by both the Government of India and Madhya Pradesh Forest Department in preparing Kuno for lion reintroduction (Johnsingh et al., 2007; Khudsar et al., 2008). Currently Kuno has been declared as an inviolate National Park (700 km^2) after the resettlement of 24 villages (1,547 families). A financial investment of about Rs 15 crores (US$ ca. 3.2 million) was done by the Government of India until 2005 for resettlement and management of Kuno (Johnsingh et al., 2006) and an equal amount invested by the Government of Madhya Pradesh. Subsequently, a buffer area of 1,280 km^2 has been added to the Kuno National Park as Kuno Wildlife Division. Better protection, habitat management, and relocation of human settlement along with majority of their livestock, resulted in a substantial recovery of the wild ungulate population. The chital population have exponentially increased from a density of 5 to 68/km^2 within the past 10 years (Banerjee, 2005; Bipin et al., 2013).

Gujarat monopolized Gir lions after they were stripped off their status as India's National Animal in 1973. Lions were promoted as a Gujarat State icon which soon became engrained as a symbol of the pride of the people of Gujarat (Rangarajan, 2001). Indeed, it was due to the efforts of the people of Gujarat that lions have shown an extraordinary recovery for any large carnivore. The local media exemplified and promoted this monopoly (Rahmani, 2013) which was subsequently used as an instrument of political and bureaucratic gain (Dutta, 2019). This new found exclusive ownership of the lions by Gujarat State and its bearing on the public psyche resulted in the Gujarat Government's reluctance to provide a founder stock of wild lions to the State of Madhya Pradesh (Kuno). The Gujarat Forest Department, which is the technical arm of the State Government in matters of wildlife, posed trivial arguments against reintroduction of lions in Kuno (Singh, 2007). However, a landmark judgement was passed by the Supreme Court of India in 2013 [IA No.100 in W.P (C) No.337/1995, accessible at http://www.conservationindia.org/wp-content/files_mf/Lion-judgment-SC-Apr-2013.pdf] which directed the Governments of India, Gujarat and Madhya Pradesh to reintroduce lions in Kuno despite contrary arguments of Gujarat. Although this landmark verdict by the apex court was primarily directed toward lion reintroduction, it recognized conservation as an integral part of civilized development and beckoned for applying the "species' best interest standard" for conservation of lions and other endangered species. This judgement strongly places the responsibility on the national and state governments, together with the citizens, to view development through an eco-centric approach and not just with an anthropocentric perspective.

As per the assessment of the committee for lion reintroduction appointed by the Supreme Court through their court order, Kuno National Park can currently hold about 40 lions. The larger forested landscape of about 3,000 km^2 around Kuno, has the potential to support a viable lion population for the long-term. The Kuno lion reintroduction action plan (Ministry of Environment Forests and Climate Change [MoEFCC], 2016) is in consonance with the IUCN/SSC reintroduction group guidelines (IUCN/SS, 2013) and provides operational guidelines to the wildlife managers of Gujarat and Madhya Pradesh States to implement the reintroduction and subsequent management of the lion population. Despite the direction of the Supreme Court in 2013 and an action plan (Ministry of Environment Forests and Climate Change [MoEFCC], 2016) with a clear vision, the reintroduction program is facing a socio-political deadlock for the past 6 years. The program implementation is still being debated between the Ministry of Environment, Forests and Climate Change, Government of India; Gujarat Forest Department; and the Madhya Pradesh Forest Department.

While lion reintroduction in Kuno was being debated, the Gujarat Forest Department mandated the Wildlife Institute of India to evaluate the potential of Barda Wildlife Sanctuary (**Figure 2**) as another reintroduction site for lions within Saurashtra, Gujarat. Barda and its adjacent Alech hills (Barda landscape) had lions until the late nineteenth century after which they were locally extirpated (Divyabhanusinh, 2005). Subsequent conversion of forest and grazing lands to agriculture separated Barda from Gir (~80 km). This less permeable habitat matrix along with the initial policy of the Gujarat Forest Department to capture dispersing lions and relocate them back to Gir, prevented recolonization (Ranjitsinh, 2016). The assessment of Barda (Jhala et al., 2014b) suggested that the landscape (410 km^2 comprising of 190 km^2 of Barda WLS, Alech hills and coastal forest patches) could sustain about 25 lions after creating an inviolate area of about 100 km^2 within the Barda WLS, restocking prey, enhancing protection, and restoring habitats. Currently the sanctuary is inhabited by about 1,325 families of *Maldharis* in 62 *ness*es and 98% of them are willing to resettle outside Barda (Jhala et al., 2014b). The costs of incentivised, voluntary relocation (Narain et al., 2005) would be close to Rs 200 crore (US$ ca. 28 million). Current wild prey density in Barda is very low and inadequate for sustaining even a single lion pride, but livestock and scavenging opportunities abound. Resettlement of human habitation and building up wild prey is likely to take several years. Establishing a lion population in Barda landscape would be beneficial for lion conservation as well as help conserve the native flora and fauna of this region which is threatened by intense human exploitation. However, a lion population in Barda cannot be considered as a security from catastrophic events like disease epidemics in the Gir landscape due to the geographic proximity of both areas and continuous presence of feral dogs, cats, and livestock in the intervening habitat. Barda, therefore cannot be an alternative solution to lion reintroduction in Kuno (Jhala et al., 2014b). Efforts of the Gujarat Forest Department in conserving a representative lion gene pool through conservation breeding programs (Meena and Kumar, 2012) are important initiatives to pre-empt a catastrophic extinction event within the Gir landscape. However, carnivores bred in captivity over several generation are usually unfit for reintroductions into the wild (Jule et al., 2008). Therefore, we submit that the "species best interest" strategy for securing Asiatic lions in the long-term would be to establish as many free ranging populations as possible within the historic range of the Asiatic lions. Founders for such populations should be sourced from wild Gir lions to capture their existing genetic diversity and subsequently managed as a metapopulation with the Gir lion population (Ministry of Environment Forests and Climate Change [MoEFCC], 2016).

Management Interventions

The contribution of wildlife managers has been the most vital ingredient for the conservation of Asiatic lions. Wildlife management in India is done by the respective State Forest Departments. Their primary role is to manage the PAs in terms of administration, law-enforcement, wildlife conflict mitigation, habitat management, and management of wildlife tourism. Other aspects include community participation through incentives by sharing park revenues in the form "eco-development projects," sensitization of local communities through awareness and education camps, treatment and rescue of wildlife. In this section we succinctly portray the management arena for Gir PA and discuss their strengths and weaknesses under the larger gambit of lion ecology and conservation, tethering with our previous sections.

The total strength of the wildlife department of Gir PA in 2012 was about 688 (Meena and Kumar, 2012). Modern amenities in the form wireless service, good road network, 4- and 2-wheel drive vehicles and arms are available and used by the wildlife authorities. Regular patrolling on-foot and by vehicles has controlled poaching within PAs. However, snaring and electrocution continue to be a major concern for wildlife authorities in the larger landscape. Eight lions were poached in 2007 for meeting the illegal demand of lion bone trade (Singh, 2017b). The wildlife authorities successfully nabbed the poachers and got them convicted in the court of law under the Wildlife (Protection) Act 1972 setting an example that has deterred poaching of lions to a great extent.

The wildlife department has developed competence in veterinary facilities for treating animals in distress at eight facilities across the Gir landscape. Also, lions in conflict or individuals straying into human-habitation too often are captured and rehabilitated. Perception of the public and media to an ailing/injured lion forces wildlife authorities to capture and treat such animals. Within the past decade, medical interventions for treating even minor injuries and ailments in lions have become the norm. As discussed earlier, such actions can tamper with the process of natural selection, and should be undertaken judiciously. The reluctance of wildlife authorities in seeking expert advice on dealing with dangerous situations like CDV outbreaks can have disastrous impacts on the long-term survival of this single population of Asiatic lions.

Gir being a dry deciduous forest tract, water is a major factor that limits the abundance and distribution of animals. Wildlife authorities manage the availability of water in the landscape through provisioning by regular maintenance and filling of artificial waterholes. Weed and invasive species removal is done across the PA, and an area of over 270 km^2 was prescribed for treatment (Meena and Kumar, 2012). Gir PA is prone to fires and the regular management of ∼1,900 km of fire-lines is done annually to contain accidental fires (Meena and Kumar, 2012).

Lion centric tourism within Gir PA is an important source of revenue for the Gujarat Forest Department and about 0.12 million tourists visited Gir PA annually in between 1995 and 2010 (Meena and Kumar, 2012). The number of tourists has substantially gone up in the recent years (0.533 million in 2015 and 0.522 million in 2016). The Forest Department permits tourism in a part of the western Gir WLS by allowing tourist vehicles (accompanied by trained nature guides) to ply over forest roads in eight pre-fixed routes (ranging from 22 to 45 km) after obtaining online permits. In order to reduce tourism pressure inside the Gir PA and to provide tourists with guaranteed opportunities of viewing lions and other wildlife, two safari parks (each of about 4 km^2, enclosed by chain-link fences); at Devalia (western Gir) and Ambardi (eastern Gir) have been created that house semi-free ranging wildlife including lions. All these activities generate a substantial amount of revenue. For example, in 2016 revenue generated from gate fees was Rs. 102.5 million (∼ 1.5 million US$, https://timesofindia.indiatimes.com/city/ahmedabad/gir-sanctuary-collects-its-highest-ticket-revenue-ever/articleshow/61108927.cms). However, as mentioned earlier, practice of luring lions with artificial subsidies such as carcasses to maximize lion viewing by tourists (Gogoi, 2015) should be discontinued.

With the increase in the extent and magnitude of lion-tourism, hospitality industry has flourished along the periphery of the Gir PA. Within a six-km radius of the tourism circuit of the PA, there are nearly 100 resorts, hotels and guesthouses catering to the needs of tourists. Many such facilities have been totally or partially shut down following a *suo motu* Gujarat High Court order against illegal and haphazard construction around Gir PA. Meanwhile, the Government of Gujarat has submitted an eco-tourism policy to the High Court proposing to: (i) decline new licenses for hotels and resorts within 1 km of the Gir PA and (ii) levy a new tax known as "eco development fee" for conversion of agricultural land to commercial tourism purposes.

With the objective to sensitize the younger generation toward wildlife conservation, nature camps are conducted by the Gujarat Forest Department since 1976. Students from local schools and colleges camp at five designated sites in the PA and are taken on field excursions with trained nature interpreters, interact with wildlife managers through illustrated talks and field demonstrations, and are shown wildlife documentaries (Meena and Kumar, 2012). Additionally, eco-clubs have been established in about 300 schools within the Gir landscape with the aim of spreading awareness related to nature conservation in their localities. The Government tourism facility at Gir has a good interactive interpretation center that is popular amongst the visitors of the park.

In order to garner public support for lion conservation, an "eco-development" scheme was initiated in Gir along with six other PAs in India under the India Eco-development Project funded by World Bank's Global Environment Facility. A total of 193 villages have so far been covered in the landscape under this scheme (Singh, 2017a). Under this scheme, repair of village roads, support for self-employment, construction of structures for harvesting water and preventing soil erosion, facilities for education, drinking water, sanitation and improvement of houses are provided and linked to wildlife conservation. Parapets were constructed for about 25,000 open wells that otherwise act as death traps to lions and other wildlife. Members of the local community that have demonstrated wildlife skills are designated as *vanya prani mitra* (friends of wildlife) and paid a nominal remuneration for assisting with wildlife management activities of the park managers (including information on poaching, fire management, and wildlife conflict resolution). Besides the monetary remuneration, the enhanced social status of the *vanya prani mitra* is an incentive for community members to strive to become "wildlife friends." An average amount of Rs. 8.36 million (~122,139 US$) was spent by the Forest Department for accomplishing various activities under this scheme between 2006 and 2010.

Another major activity undertaken by wildlife managers is the 5 yearly periodic population enumeration of lions. This exercise is commendable in its extent, effort, and regularity. However, as previously mentioned, the archaic approach of population census through total counts needs to be replaced with modern scientific approaches of animal abundance estimation that explicitly address the issue of detectability and double counts. Such a scientific assessment by an independent agency would also preclude the potential of distorting numbers to create *political populations* (Darimont et al., 2018) as was done earlier with tiger populations in India (Karanth et al., 2003).

CONCLUSION

The recovery of the Asiatic lion in the Saurashtra landscape is a success story and lauds the efforts of the native rulers and the republic Governments of India and Gujarat. The exemplary coexistence between lions and the people of Saurashtra provides the world with a plausible model and after addressing the caveats mentioned above, can be replicated in other areas. The most important ingredient that sets the stage for this coexistence is the traditional value of reverence toward lions and other life forms. Yet, in a changing world of values, economic profits related to livelihoods derived directly or indirectly from lions played a significant role in promoting coexistence. The current stand of authorities in accordance with the Wildlife (Protection) Act 1972, is to ban lion shows, since there are currently no mechanisms for regulating them. However, these shows are a major source of direct profits for local communities. Despite the negative aspects of lion shows, we believe that they provide a window of opportunity for a paradigm shift in the conservation ethos in India. We propose that wildlife authorities should take the initiative to work with elected representatives of the local community (village panchayats) to form consortia of one to several villages across the landscape to form "Community Lion Conservancies (CLCs)." These CLCs would then formulate guidelines for lion based ecotourism in accordance with the Wildlife (Protection) Act 1972, in consultation with the Forest Department and NGO's. The principles for profit sharing from lion shows should be equitable unlike the present despotic system where profits are monopolized by socially powerful elements of the community. A potential mechanism for equitable sharing of profits while retaining individual incentives would be to use majority of the revenue in community upliftment activities (such as better health-care, sanitation, education etc.), while a small fee is paid to the land owners who manage their lands in a lion-friendly way to promote such ecotourism opportunities. Lion ecotourism operated and regulated on such principles would ensure that existing laws are not violated, lions are not harassed, allow wildlife authorities to keep check on such activities on private lands, while profits are shared amongst the entire community thereby promoting goodwill and support for lion conservation across all sections of the society. Once legally recognized and benefits are directly associated with lions, we believe that communities will protect and promote lions and their habitats in CLCs and can also locally pay compensation for livestock predation events to bridge the gap between Government compensation and market price. In densely populated countries like India where creating large PAs is difficult, conserving lions as well as other wildlife in human dominated landscapes is essential to house viable populations. Co-occurrence is bound to create conflict. Good innovative management practices to promptly address these conflicts along with economic incentives to local communities is the only way to ensure continued tolerance toward large carnivores in such landscapes. Formalizing and legally recognizing profits from wildlife with appropriate controls through the proposed CLCs will be a major paradigm shift for conservation in India.

The only source population of Asiatic lions is within the Gir PA. To preserve the lions' ecological role and evolutionary potential it is important that a substantial population is maintained in its natural setting. Thus, it is important to expand the National Park to create an inviolate habitat of 800–1,000 km^2 for lions, as is recommended for tiger reserves in India. In the human dominated landscape of Saurashtra, all habitat patches larger than 4 km^2 (**Figure 2**) should be targeted for protection and conservation, as these serve as breeding refuges and are vital elements for lion persistence in the landscape. Development within the identified lion movement corridors should be curtailed and linear infrastructure traversing such corridors must be mitigated with animal passageways.

Establishing a second free-ranging lion population away from Gir should be the most important conservation priority for the species. Kuno is an ideal option in a state that has a proven track record for tiger conservation. Substantial investments have already been made in Kuno which is ready to receive the founding stock of lions. It is unfortunate that due to overly enthusiastic zeal of ownership and monopoly of the people of Gujarat, the Asiatic lions are caught in a socio-political deadlock that prevents this essential reintroduction program, despite a clear directive of the Supreme Court of India.

Conservation of Asiatic lions is thus a conundrum with an admixture of contradictions and improvisations. Based on information accrued from our long-term research added to past knowledge, we demonstrate that conservation of a species so deeply engrained in human ethos and psyche not only requires appropriate scientific knowledge of its ecology but also a multidimensional understanding that encompasses history, culture, economics, and politics for its holistic management. We reiterate that only through the continued *nurture* of Asiatic lions and other wildlife would their *nature* be fully safeguarded in a country like India that teems with people and biodiversity.

AUTHOR CONTRIBUTIONS

Author sequence is in order of their contribution to this research and review. YJ conceived the research project and raised resources, supervised field work, logistics, and data collection. YJ, KB, SC, PB, KS, CD, and KG collected and analyzed primary data pertaining to different components of the long-term research project. YJ, KB, and SC reviewed pertinent literature and wrote the manuscript. YJ, KB, SC, and KG prepared the maps and figures for the manuscript. All authors read and commented on the initial drafts of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00312/full#supplementary-material

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