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REVIEW

Review of the global research on Hyaenidae and implications for conservation and management

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ABSTRACT

1. Despite the ecological importance of the four extant species of Hyaenidae, and the threats they face globally, there has been no review of the nearly 100 years of published research on hyaenas, nor has there been a synthesis of management-related literature regarding these species.
2. We reviewed 907 studies on Hyaenidae, summarized broad temporal, geographic and topical trends, and evaluated findings from management-related research to determine ways forward for hyaena conservation management. Since the first known study in 1939, most have focused on spotted hyaena (*Crocuta crocuta*; 75% of all studies), yet overall publications for Hyaenidae have increased by 372% in recent decades.
3. Only 44 of the 67 hyaena range states were represented across publications, with nearly half of all studies conducted in Kenya (18%), South Africa (16%) and Tanzania (13%). Twenty-eight countries had fewer than five studies. Ecology and diet were the most-studied topic areas. The least-studied topics were disease and physiology.
4. Studies on human–hyaena interactions were highly variable in topic, with infrastructure impacts and Hyaenidae benefits to people covered the least. All species were reported to have consumed anthropogenic diet items. Mortality data were included within 11% of publications, with 79% of recorded hyaena mortality constituting anthropogenic causes, although there were few targeted

studies on the subject. Lastly, 12% of publications involved community engagement in their methods.

5. There is a significant bias among species, topics and range states across Hyaenidae studies, and little data explicitly related to human–hyaena coexistence. Our management-focused synthesis suggests that research on Hyaenidae could better reflect large carnivore conservation and management inquiry by increasing studies focused on human interactions with Hyaenidae. To address research gaps and inform Hyaenidae management, we recommend increasing applied research outside of protected areas and using interdisciplinary, community-involved methods to increase foundational knowledge on understudied hyaena species, habitats and locations.

INTRODUCTION

Populations of mammalian carnivores are declining worldwide, and many now inhabit only small portions of their historical ranges, largely due to anthropogenic threats such as habitat loss, overharvesting, prey depletion and persecution (Ripple et al. 2014). Large carnivores are important for healthy ecosystems (Miller et al. 2001, Beschta & Ripple 2009), can serve as biodiversity indicators (Natsukawa & Sergio 2022) and fuel lucrative tourism in many locations. However, they can be difficult to study and manage since they are long lived, cryptic, typically wide ranging and often nocturnal (Barea-Azcón et al. 2007, Balme et al. 2009, Dröge et al. 2020). Large carnivores are also implicated in human–wildlife conflict, including potentially significant effects on people's livelihoods and safety (Treves & Karanth 2003), and may prey upon threatened species (Goodrich & Buskirk 1995), contributing to negative human perceptions that underpin the complexity of carnivore management (Lozano et al. 2019).

The four extant species of the family Hyaenidae – aardwolf (*Proteles cristata*), brown hyaena (*Parahyaena brunnea*), spotted hyaena (*Crocuta crocuta*) and striped hyaena (*Hyaena hyaena*) – are no exception to these research and management complexities. Hyaenidae includes three of the world's large terrestrial carnivores (brown, spotted and striped hyaena), and a nearly obligate insectivore (aardwolf), although in the fossil record, hyaenids were an exceedingly diverse group comprising nearly 100 species (Werdelin & Solounias 1991). For the extant species, research on topics ranging from the evolution of social intelligence in spotted hyaena (Holekamp et al. 2007) to the insectivorous adaptations of the aardwolf (Cooper & Skinner 1979) has expanded our knowledge of many seminal biological and ecological phenomena. The spotted hyaena, in particular, is a generalist species that is widespread across many different habitats (Watts & Holekamp 2007) and has advanced our understanding of predator–prey interactions (Holekamp et al. 2009) and the sheer breadth of foraging strategies that one species may employ in different contexts (Holekamp & Dloniak 2010, Yirga et al. 2015). Studies focused on interactions between hyaenids and other carnivores have also yielded valuable insight into how hyaena behavioural ecology may drive broader carnivore guild interactions (Cooper 1991, Trinkel & Kastberger 2005, Green et al. 2019). Meanwhile, the aardwolf relies upon an ecosystem engineer of high conservation importance – the termite (*Trinervitermes* spp.; Cooper & Skinner 1979) – as its primary food source and has been listed as a high conservation priority because of its unique genetic makeup (Dalerum 2013). Overall, given their broad representation of ecological niches and flexibility in habitat needs, along with their potential roles in disease regulation, the four species of Hyaenidae serve as important contributors to ecosystem health (Mills & Hofer 1998).

Like many other large carnivores, threats to hyaena are diverse and include habitat loss and fragmentation, declining prey populations and conflicts with humans (Mills & Hofer 1998, Ripple et al. 2014, Green 2015). Habitat degradation and prey depletion may constitute significant ultimate threats to hyaena species (McFadden 2022), while often contributing to human–hyaena conflicts such as poisoning, spearing and other forms of persecution. The diversity of life-history strategies among the Hyaenidae also contributes to the variety of relationships these species have with humans (Mills & Hofer 1998). For example, spotted hyaena are behaviourally plastic apex predators, scavengers and opportunists (Holekamp et al. 2012, Pereira et al. 2013). Thus, their potential food sources are diverse, and they can predate on domestic animals (Kissui 2008, Yirga et al. 2015), occasionally attack people (Baynes-Rock 2015, Abebe et al. 2020) and will scavenge on human remains (Gade 2006). Additionally, while striped and brown hyaena are known to scavenge, they may also prey upon ungulates, including livestock (Leakey et al. 2002, Weise et al. 2015), and can have nuanced relationships with and abilities to adapt to humans. For example, brown hyaena consume livestock carcasses and human-generated refuse without necessarily incurring human–hyaena conflicts (Maude & Mills 2005), while striped hyaena can also persist within human-dominated landscapes, with predictable anthropogenic food sources as a key correlate of conflict (e.g. Bar-Ziv et al. 2022).

Brown, spotted and striped hyaena (the three bone-cracking hyaena species) are thus extensively associated with both realized and perceived human–hyaena conflict throughout their range (AbiSaid & Dloniak 2015, Bohm & Höner 2015, Wiesel 2015), with one documented example for aardwolf (Yarnell & MacTavish 2013). These complexities contribute to the bone-cracking hyaena species being the target of often overwhelmingly adverse human sentiments (Macdonald et al. 2022), while the aardwolf faces human misconceptions (such as mistaken identity) that can impact its survival (Green 2015, Rust & Taylor 2016, Monsarrat & Kerley 2018). Notwithstanding these human-oriented challenges, there remains a lack of empirical data regarding the effectiveness of interventions designed to reduce human–carnivore conflicts (Van Eeden et al. 2018), including human–hyaena conflicts. Furthermore, human–hyaena interactions are not ubiquitously negative, yet neutral and positive interactions are rarely discussed. For instance, scavenging by spotted hyaena may result in considerable benefits to human and livestock health and local economies by serving as endpoints for some diseases, such as anthrax, bovine tuberculosis and rabies (East et al. 2001, Sonawane et al. 2021), and potentially through translating an understanding of their strong immune systems (Flies et al. 2015, 2016) into implications for human immunology. Therefore, empirical research on human–hyaena interactions, aimed towards coexistence and inclusive of community members dealing with real and perceived conflicts, is of paramount importance for informing management decisions.

Despite the challenges of doing field research on large carnivores and the generally negative public perceptions of hyaena species, there is a rich history of scientific research on Hyaenidae. In particular, the ubiquity, unique social organization and female masculinization of the spotted hyaena have fuelled several long-term research projects. Pivotal spotted hyaena research programmes located in Tanzania, Kenya, and the United States (a captive programme) have examined the evolution of sociality and predator–prey interactions, along with physiology, behaviour, development and ecology, providing rich understanding of basic spotted hyaena biology across a range of contexts (Kruuk 1966, Frank 1997, Holekamp et al. 1997, 2012, Hofer & East 2003, Glickman et al. 2006, Holekamp & Strauss 2020). There have also been important ecology- and demography-focused research projects on brown hyaena in Namibia, South Africa and Botswana (e.g. Maude & Mills 2005, Wiesel et al. 2019) and striped hyaena in Kenya and Nepal (e.g. Wagner et al. 2007, Bhandari et al. 2021). Meanwhile, there is only one established research project on aardwolf (Anderson & Richardson 2005). Yet, most of these established projects have broadly focused on ecology and behaviour, with less emphasis on applied topics such as anthropogenic threats and human–hyaena interactions.

As we navigate a world increasingly dominated by humans (Lewis & Maslin 2015), management of hyaena and other large carnivores will best be informed by the global body of research on these species. There are many arguments for ‘keeping common species common’ (Frimpong 2018) – which applies to at least two of the species in Hyaenidae – and for being proactive rather than reactive about the management of large carnivores due to their roles as biodiversity indicators (Natsukawa & Sergio 2022) and ecosystem service providers, along with their inevitable interactions with people (Chapron & López-Bao 2016). Yet despite their ecological importance and the decline in populations of some Hyaenid species, there is no recent review of the >80 years of published science regarding Hyaenidae, nor has there been a detailed synthesis of the conservation management research and its implications for these species. Towards these aims, here we 1) review the published literature on extant species of Hyaenidae to identify broad temporal, geographic and topical trends per species and as a whole; 2) synthesize the research on topics pertinent to conservation management in particular (specifically, human–hyaena interactions, anthropogenic diet items, mortality sources and community-inclusive methods); and 3) determine implications of our results for future research and global management of these species.

METHODS

Data collection

We conducted a literature search on Web of Science (https://www.webofknowledge.com) in the Web of Science Core Collection (1900–present) on April 21, 2022, using scientific and English common names of all four extant species (Appendix S1), with no start date restrictions. Additionally, papers were added manually if they were known to any of the authors but missed in the initial search or published through August 2022. Publications were selected for detailed review if they contained 1) newly presented data about at least one of the four extant hyaena species, or 2) a meta-analysis or synthesis of existing research on any of these four species. For publications on multiple hyaena species, we extracted species-specific information and included it in the synthesis for that individual species.

Data categorization and analysis

CATEGORIZATION

We categorized each publication according to its focal species, geography, method and topic (Table 1). For studies containing field research (hereafter, 'field studies'), we noted the range state where the research occurred. Whenever possible, we examined whether the research occurred in a protected area (including multi-use protected areas), outside of a protected area or both. Research that exclusively occurred in lab/captive settings was excluded from calculations involving geography. Research foci were categorized across 67 specific topics which were framed as 11 topics: 1) behaviour and cognition; 2) disease; 3) ecology and diet; 4) endocrinology, morphological development and anatomy; 5) genetics; 6) human impacts, conflicts and benefits; 7) interspecific interactions; 8) movement, activity and territoriality; 9) physiology; 10) population and range; and 11) sexual selection and mate choice (Table 1). The 'human impacts, conflicts, and benefits'

Table 1. Data categorization for papers concerning extant species of Hyaenidae, specifically (A) classification of geography, methods, publication type and species concerned, and (B) the broad topics focused upon within the publications

A

Broad category	Specific category
Geography	Continent, Country, State/Province/County, Specific location, inside of protected area (including multi-use protected areas such as conservancies) vs. outside of protected area
Methods	Callbacks or acoustic observations, Camera traps, Direct observation, GPS/radio collars, Interviews/participatory/Traditional Ecological Knowledge [community engagement], Hyaena prey remains, Hyaena roadkill/carcass/remains, Samples taken (tissue, hair, blood, paste, etc.), Scat, Tracks
Publication type	Book/book chapter, Conference proceedings, Journal article, Report, Review, Short communication, Thesis
Study species	Aardwolf, Brown hyaena, Spotted hyaena, Striped hyaena
Target or non-target species	Target (the study was primarily focused on one or more extant hyaena species), Non-target (the study was primarily focused on a species other than an extant hyaena species), Both (the study was focused on multiple species including one or more extant hyaena species)

B

Broad topic	Specific topic
Behaviour and cognition	Cognition (general), Evolution of behaviour, Intraspecific cooperation, Intraspecific competition, Novel objects, Plasticity, Play behaviour, Puzzles, Sociality (generally)
Disease	Disease (general), Disease negative impacts, Disease resistance, Interspecific disease transmission, Intraspecific disease transmission, Parasites
Ecology and diet	Coprophagy, Denning characteristics or behaviours, Foraging, Gut and/or body microbiome, Habitat suitability, Natural death, Predation, Scavenging *Specific diet items categorized: Bird, Human refuse, Human remains, Insect, Livestock, Marine and/or aquatic prey, Reptiles and amphibians, Vegetation, Wild terrestrial prey (non-insect, non-avian)*
Endocrinology, morphological development, anatomy	Anatomy, Endocrine status (general), Foetal and young development, Reproductive hormones, Siblicide/sibling competition, Stress hormones
Genetics	Gene flow, Maternity/paternity, Taxonomy/phylogeny
Human impacts, conflicts, benefits	Anthropogenic impacts (general), Fence impacts, Fence navigation, Fragmentation, Human hunting of hyaena, Human-caused death, Human–hyaena interaction and conflict (generally), Local attitudes/perceptions, Poisoning/toxicity, Public health, Road impacts, Road navigation, Snares, Witchcraft/spiritual roles and uses
Interspecific interactions	Interspecific competition or threats, Interspecific cooperation, Non-predation interactions with herbivores
Movement, activity, territoriality	Dispersal/immigration, Movement, Scent marking, Temporal activity patterns
Physiology	Energy expenditure, Feeding physiology, Locomotion, Metabolic rate
Population and range	Density, Demography, Distribution and home ranges, Population (–), Population (+), Population trends (general)
Sexual selection and mate choice	Courtship behaviour, Intersexual competition, Intrasexual competition (i.e. infanticide, hazing, etc.), Reproductive success

category, on which we spend much of our focus in this paper, included topics related to human–hyaena interactions, hyaena impacts on and benefits to public health and human well-being and hyaena interactions with human infrastructure. We also noted if each publication contained mortality records, threat data or specific diet item information. We compiled data on mortality sources within studies published from 1998 onwards to follow the status survey conducted by Mills and Hofer (1998). Diet items were further classified into the following nine categories: birds, human refuse, human remains, insects/arachnids, livestock, marine/aquatic prey, reptiles/amphibians, vegetation and wild terrestrial mammalian prey. Lastly, we categorized the research methods used for each study using the following: callbacks or acoustic observations, camera traps, direct observation, GPS/radio collars, interviews or traditional ecological knowledge, hyaena prey remains, hyaena roadkill/carcasses, samples (blood, tissue, etc.), scat and tracks (Table 1).

Mortality records were categorized according to the generic (anthropogenic or natural) and specific causes of mortality (Appendix S1) and were grouped into three categories: 1) *anecdotal mortality records*, which consisted of singular mortality incidents recorded opportunistically without a wider context; 2) *contextual mortality records*, which consisted of mortality recorded systematically in a wider context and/or longitudinally; and 3) *human impact/threat record*s, in which people described or engaged in lethal activities towards hyaena. Mortality records were also assessed as to whether they occurred in a protected, unprotected or partially protected (encompassing both types of land) area if sufficiently precise geographic data were given in the publication or could be deduced.

ANALYSES

We used Friedman's rank-sum test (Pereira et al. 2015) and chi-square tests to evaluate differences in studies conducted for each species overall and in relation to topics, methods, geography and protected area status. To test the association between species and broad focal topics represented in the published literature, we used R package *MASS* (Ripley et al. 2013) to create an independent (i.e. species and topic covered assumed mutually independent) and a saturated (i.e. species and topic covered associated with one another) log-linear model for all species and topics. We then compared the performance of these two models using Akaike's information criterion (AIC) – with the better-performing model having a lower AIC value (Burnham & Anderson 2002) – and a likelihood ratio test (using R package *lmtest*), and used the odds ratios of the higher performing model to assess differences in the odds of a topic being disproportionately covered for each species. We used proportion tests to analyse within-species differences in reported diet items and conducted exponential regression models to analyse trends in the number of studies per year for each species. Finally, we used descriptive statistics to illustrate the inclusivity (i.e. community engagement) of methods and the interdisciplinarity (i.e. whether two or more broad topics were covered) of studies that included community engagement. All statistical analyses were conducted using R version 4.2.2 (R Core Team 2022). Additionally, to contextualize the studies on Hyaenidae conducted within and outside of protected areas, we used the World Database of Protected Areas (WDPA; UNEP-WCMC & IUCN 2022) and the 2015 IUCN Red List Assessment range maps to calculate the proportion of each species' range comprised of designated IUCN (categories 1–4) protected areas using ArcGIS Pro 3.0.2 (Esri Inc 2022).

RESULTS

Geographic, temporal and topical trends in Hyaenidae literature

The literature search yielded 1392 publications, of which we retained 907. We excluded publications that did not concern or mention one or more of the four extant Hyaenidae species. Of the unretained publications, 179 were excluded from analyses because they primarily concerned extinct hyaena species.

Of the 907 retained publications, 9% ($n = 84$) contained information on multiple hyaena species and 715 (79%) included field studies. There was a significant difference in the total number of studies conducted across the species (Friedman rank-sum test; d.f. = 3; $\chi^2 = 25.36$; $P < 0.001$), with the spotted hyaena appearing in the highest number of publications ($n = 684$, 75% of all publications), followed by striped hyaena ($n = 161$, 18%), brown hyaena ($n = 130$, 14%) and aardwolves ($n = 67$, 7%). Of these, there were 44 field studies on aardwolves, 95 on brown hyaena, 519 on spotted hyaena and 117 on striped hyaena.

GEOGRAPHY

Of the 67 Hyaenidae range states, 66% ($n = 44$) had at least one hyaena-related publication (Fig. 1). The majority of field studies were conducted in three African countries: Kenya ($n = 166$, 18% of all studies), South Africa ($n = 147$, 16%) and Tanzania ($n = 118$, 13%), with significant geographical biases in study sites across all species ($\chi^2 = 814.77$, d.f. = NA [simulated P-values], $P < 0.001$). Sixteen range states were only associated with one field study each. The

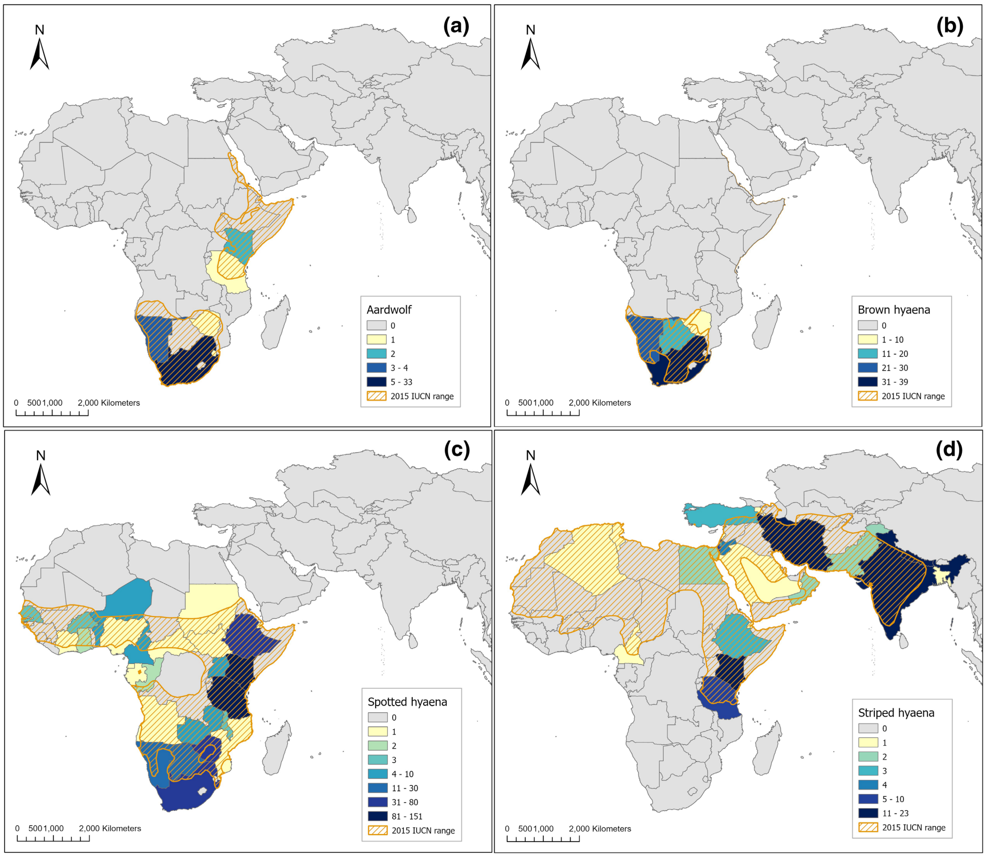

Fig. 1. Maps of publications retained for this review concerning (a) aardwolf, (b) brown hyaena, (c) spotted hyaena and (d) striped hyaena, overlaid by the 2015 IUCN ranges for each species.

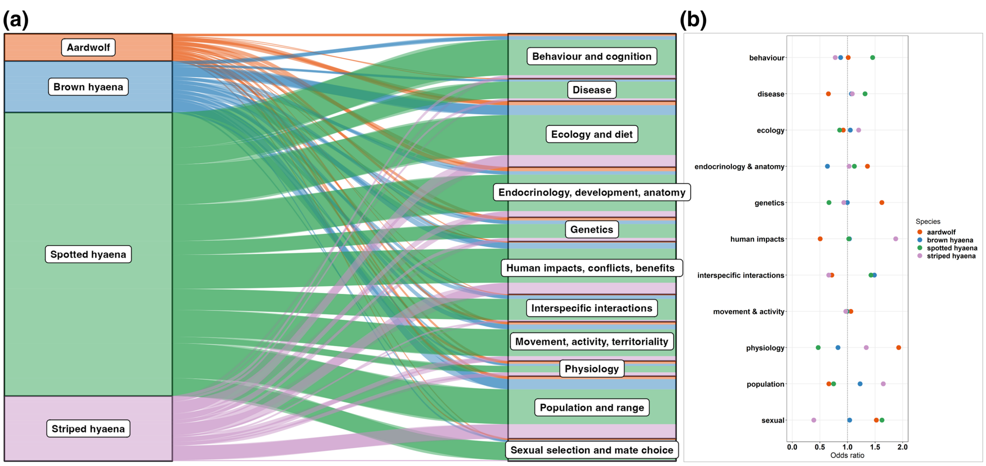

Fig. 2. (a) Distribution of broad topics by hyaena species, in which colours are designated based on species, and the relative size of the different sections in the two axes for species and broad topics are scaled according to sample sizes, and (b) results from a saturated log-linear model, demonstrating odds ratios for broad topics covered for each hyaena species, in which values above 1 indicate the topic is more likely to be covered in the literature for that species and values below 1 indicate the topic is less likely to be covered in the literature for that species.

best-represented country for field studies on aardwolves ($n = 33$, 49% of total aardwolf publications) and brown hyaena ($n = 39$ field studies, 30% of total brown hyaena publications) was South Africa (Fig. 1, Appendix S1). Most spotted hyaena field studies were conducted in Kenya ($n = 151$, 22% of total spotted hyaena publications), Tanzania ($n=109$, 16%) and South Africa ($n=70$, 10%), and the best-represented locations for field studies on striped hyaena were Kenya and India (14% each of total striped hyaena publications) (Fig. 1, Appendix S1).

TOPICAL FOCI

Generally, there were differences in the number of studies conducted on the 11 broad topics when compared to expected values (Appendix S1: Fig. S5). When assessing the independent and saturated log-linear models on broad topics covered by species, the saturated model (i.e. interaction between species and topic) showed better performance than the independent model (likelihood ratio $\chi^2=131.06$, d.f. = 30, $P<0.001$). Within this model (all coefficients and odds ratios listed in Appendix S1), the most notable elements were that spotted hyaena studies were significantly less likely to cover genetics (OR = 0.62, 95% CI = 0.13–0.66) or physiology (OR = 0.4, 95% CI = 0.07–0.47) than other topics, and striped hyaena studies were significantly more likely to cover human impacts/conflicts/benefits (OR = 1.87, 95% CI = 1.74–14.17) or population/range (OR = 1.65, 95% CI = 1.29–8.18) than other topics (Fig. 2), although the precision was notably lower for striped hyaena studies. Additionally, over half (57%, $n=38$) of aardwolf studies, 58% ($n=75$) of brown hyaena studies, 61% ($n=415$) of spotted hyaena studies and 59% ($n=95$) of striped hyaena studies were interdisciplinary (i.e. concerned at least 2 of the 11 broad topics).

AARDWOLF

The most-studied broad topics regarding aardwolves were ecology/diet and endocrinology/morphological development/anatomy, while the least-studied broad topics were disease, interspecific interactions and human impacts/conflicts/benefits (Table 2, Fig. 2). Specifically, most studies focused on anatomy, taxonomy, phylogeny, evolution and foraging (Appendix S1). There were no studies conducted on the following specific topics: disease transmission and negative impacts, human infrastructure navigation, immigration and dispersal and novel object and puzzle exposure (Appendix S1).

Table 2. Broad topics covered by studies conducted on each species, and percentage of total studies on each species comprised by studies on that topic

	Aardwolf: count	Aardwolf: % of studies	Brown hyaena: count	Brown hyaena: % of studies	Spotted hyaena: count	Spotted hyaena: % of studies	Striped hyaena: count	Striped hyaena: % of studies
Behaviour and cognition	12	18	19	15	182	27	18	11
Disease	4	6	12	9	85	12	13	8.1
Ecology and diet	24	36	50	38	235	34	61	38
Endocrinology, morphological development, anatomy	21	31	18	14	183	27	31	19
Genetics	16	24	18	14	69	10	18	11
Human impacts, conflicts, benefits	8	12	30	23	171	25	58	36
Interspecific interactions	5	7.46	19	15	105	15	9	5.59
Movement, activity, territoriality	14	21	24	18	137	20	25	16
Physiology	14	21	11	8.46	36	5.26	19	12
Population and range	15	22	51	39	179	26	73	45
Sexual selection and mate choice	8	12	10	7.69	90	13	4	2.48

BROWN HYAENA

Most publications on brown hyaena focused broadly on population/range and ecology/diet, while the least-studied broad topics were disease and physiology (Table 2, Fig. 2). Specifically, most studies focused on distribution and home range, predation, scavenging, population trends and genetics (Appendix S1). Meanwhile, there was only one study on each of the following specific topics: evolution of behaviour, behavioural plasticity, public health, road navigation, microbiome, disease negative impacts, foetal and young development and endocrine status (Appendix S1).

SPOTTED HYAENA

Most publications on spotted hyaena focused broadly on ecology/diet, endocrinology/morphological development/anatomy and behaviour/cognition, while physiology was the least-studied broad topic area (Table 2, Fig. 2). Specifically, the most-studied topics were sociality, human–hyaena interactions and conflict, distribution/home range and anatomy, and there were very few (≤1%) studies conducted on gene flow, microbiome, play behaviour, interspecific cooperation, snares, road navigation and impacts and fence navigation and impacts (Appendix S1).

STRIPED HYAENA

Most publications on striped hyaena focused broadly on population/range, ecology/diet and human impacts/conflicts/benefits, while the least-studied broad topics were interspecific interactions and disease (Table 2, Fig. 2). Specifically, the most-studied topics were distribution and home range, anthropogenic impacts, human–hyaena interactions and conflict and habitat suitability (Appendix S1). There were no studies representing the following specific topics: courtship and intrasexual competition, sibling competition or interactions and intraspecific disease transmission (Appendix S1).

TEMPORAL TRENDS

The first documented scientific publication on Hyaenidae was in 1939 (specifically regarding spotted hyaena; Matthews 1939), and an exponential increase in yearly publications ($F_{1,54} = 255.6$, $P < 0.001$, $R^2 = 0.822$) began in the 1970s and continues to present (Fig. 3). Most recently, there was a 177% increase in publications from the decade spanning from 2001 to 2010 ($n = 213$) to 2011–2020 ($n = 377$). Publications have generally shifted from focusing on basic biology (particularly anatomy [23% of publications 1939–2000] and morphological development [18%]) and behaviour (particularly sociality [25%]) to focusing on distribution and range (24% of publications 2010–2022), human–hyaena interactions (22%) and anthropogenic impacts (19%). Studies on striped hyaena saw the greatest increase over the last two decades, with a particular focus on physiology, population/range and human impacts/conflicts/benefits – all of which saw increases of >400% when comparing 2001–2010 to 2011–2020 (Fig. 4). Meanwhile, for aardwolf, there was a 350% increase in publications on ecology and in publications on endocrinology/morphological

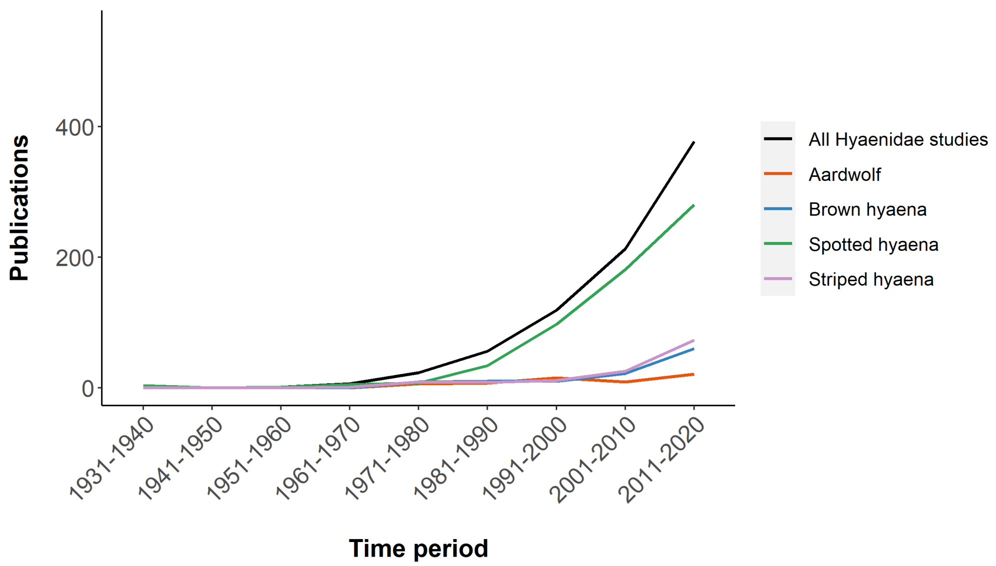

Fig. 3. The per-decade count (excluding 2021 and 2022) of all Hyaenidae publications combined and the per-decade count of publications concerning aardwolf, brown hyaena, spotted hyaena and striped hyaena, specifically.

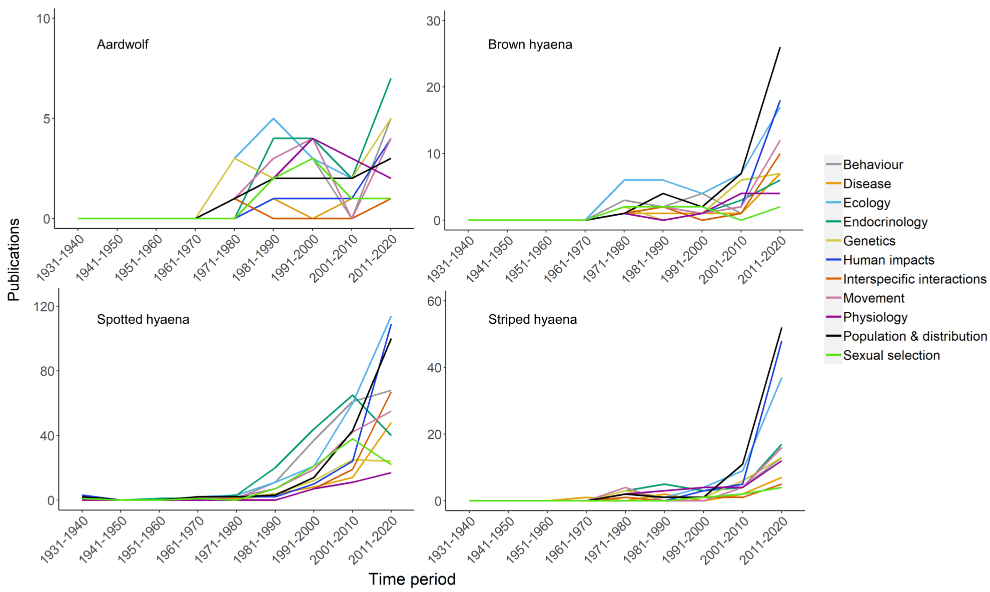

Fig. 4. The number of publications per decade (excluding 2021 and 2022) covering each broad topic for aardwolf, brown hyaena, spotted hyaena and striped hyaena.

development/anatomy. For brown hyaena, publications on interspecific interactions, human impacts/conflicts/benefits and movement/activity all saw increases of ≥600%. The most notable increases for spotted hyaenas were publications on human impacts/conflicts/benefits (454% increase) and interspecific interactions (both with increases of ≥350%), with minor decreases in publications on reproduction and endocrinology (Fig. 4).

Management, conservation and threats

HUMAN IMPACTS, CONFLICTS AND BENEFITS

A total of 235 studies touched upon human impacts, conflicts and/or benefits. Among the four species, striped hyaena had the respective highest proportion of such studies ($n=58$; 36% of striped hyaena studies) and aardwolf had the lowest ($n=6$, 9%) (Table 2). Within this broad category, human–hyaena interactions and conflict tended to be the most-studied topic (aardwolf = 3% of all aardwolf studies, brown hyaena = 12%, spotted hyaena = 16% and striped hyaena = 19%), followed by general anthropogenic impacts (aardwolf = 3%, brown hyaena = 10%, spotted hyaena = 12% and striped hyaena = 19%) (Appendix S1). Hyaena–livestock conflict ($n=48$, 45% of spotted hyaena–human interactions/conflict studies) comprised much of the human–hyaena conflict category for spotted hyaena, which was also the case for striped hyaena (29%, $n=9$), although five (5%) of spotted hyaena conflict records and two (6.5%) of striped hyaena conflict records involved attacks on people or consuming human remains. Of all species, local attitudes and perceptions were most covered for striped hyaena ($n=17$, 11%) and spotted hyaena ($n=50$, 7%). Meanwhile, poisoning and/or toxicity and snares were poorly covered for all species (Appendix S1). Lastly, the proportion of studies on hyaena responses to and impacts from anthropogenic infrastructure and activities varied across and within species (Appendix S1). For example, 6% of striped hyaena studies ($n=10$) concerned road impacts, while only 0.6% of striped hyaena studies ($n=1$) concerned fence impacts.

STUDY AREA PROTECTED STATUS

Among all studies, 60% were at least partially conducted within a protected area. Whether a field study took place within, outside of or both within and outside of a protected area differed significantly by species ($\chi^2=85.18$, d.f. = 6, $P<0.001$; Appendix S1: Fig. S6). Studies that took place at least partially within protected areas comprised the highest proportion of field studies for aardwolf ($n=31$, 46% of all aardwolf studies), brown hyaena ($n=68$, 52%) and spotted hyaena ($n=411$, 60%), while studies taking place outside of protected areas comprised the highest proportion of studies for striped hyaena ($n=75$, 47%) (Fig. 5). However, designated protected areas comprise only 2.6%, 0.2%, 3.4% and 1.2% of the ranges for aardwolves, brown hyaena, spotted hyaena and striped hyaena respectively. Among all studies that occurred exclusively within protected areas ($n=466$), only 20% included human impacts, conflicts and benefits ($n=91$). Among studies

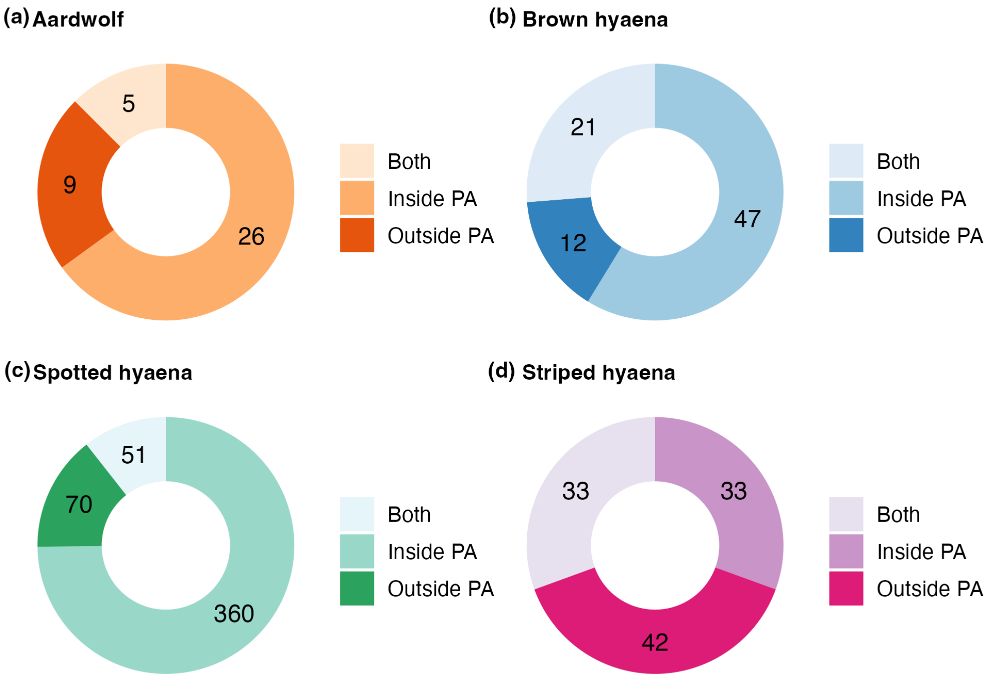

Fig. 5. Distribution of publications occurring inside of protected areas (Inside PA), outside of protected areas (Outside PA) and both inside and outside of protected areas (Both) for each of the four species in Hyaenidae, for field studies for which this information could be determined from the locations provided within the study. Labels within the plots indicate the number of publications pertaining to each category for each species.

that occurred exclusively outside of protected areas ($n=133$), 73% included human impacts, conflicts and benefits ($n=97$).

ANTHROPOGENIC DIETS

Diet was addressed in 16 (24%) aardwolf studies, 33 (25%) brown hyaena studies, 161 (24%) spotted hyaena studies and 26 (16%) striped hyaena studies. The frequency for which diet items are reported in the literature differed significantly among the four species (Appendix S1), although each diet item included in Table 1 was reported in at least one study for brown and spotted hyaena. Human refuse was the only diet category not mentioned in any striped hyaena studies, and both human refuse and reptiles/amphibians were not reported as consumed by aardwolves. All four hyaena species were recorded consuming anthropogenic diet items (Appendix S1), with livestock as the overall most-recorded prey item for striped hyaena (69% of striped hyaena studies).

MORTALITY

Of the examined publications, 82 (9%) included mortality data for at least one hyaena species, providing 183 individual records across all species. Of these mortality records, the majority were for spotted hyaena (56%), followed by striped hyaena (21%) and brown hyaena (17%), with only 8 records (4%) for aardwolves (Appendix S1). Regarding data quality, 59% of records were anecdotal, 19% included contextual mortality data and 22% concerned potential human impacts or threats, that is, people describing or described as generally engaging in lethal activities towards hyaena species (Fig. 6a, Appendix S1). Eighty-one per cent of recorded mortality was due to anthropogenic causes compared to 16% from natural causes and 4% unknown (Appendix S1). Intentional killing comprised the largest anthropogenic mortality source for all species except aardwolves, for which vehicle collisions were reported most frequently.

Across all species, 39% of mortality records were from protected areas, 31% of records were from partially protected areas and 30% of records were from unprotected areas (Fig. 6b). Within a species, spotted, brown and striped hyaena showed significant differences when comparing the number of records per protection category ($\chi^2=21.22$, d.f.$=2$, $P<0.001$, $\chi^2=14.77$, d.f.$=2$, $P=0.001$, and $\chi^2=12.05$, d.f.$=2$, $P<0.01$, respectively), while aardwolves showed no significant difference per protection category, likely due to its small sample size. The majority (54%) of spotted hyaena mortality records were from protected areas, in contrast to only 40% for striped hyaena

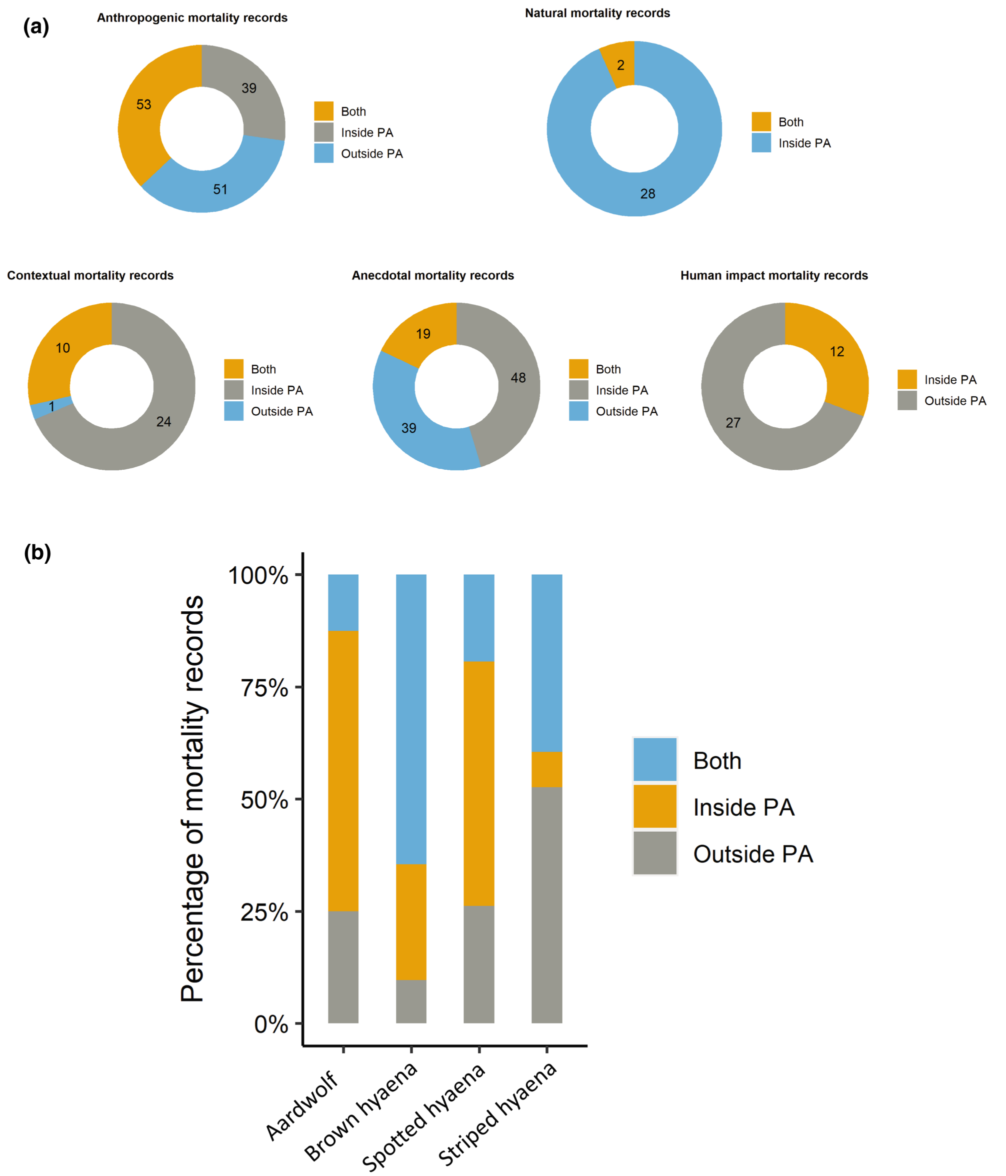

Fig. 6. (a) The number of records within and outside of protected areas with specific causes of mortality within, outside and both within and outside of protected areas for all of Hyaenidae, and (b) the proportion of mortality records for each species occurring within (Inside PA), outside (Outside PA) and both within and outside of protected areas (Both).

(Fig. 6b). Natural mortality records (Appendix S1) were nearly non-existent in unprotected or partially protected areas (Fig. 6a), with striped hyaena and brown hyaenas having one natural mortality record each within partially protected areas.

COMMUNITY-INCLUSIVE METHODS

There were significant differences in the number of studies conducted across methods for each species ($\chi^2 = 105.7$, d.f. = NA, $P < 0.001$; Appendix S1: Fig. S7). Among all studies, 12% ($n = 107$) used interviews, questionnaires and/or traditional ecological knowledge (hereafter *community engagement*) as methods. Community engagement was used for 38% of the 232 studies that focused on research related to human impacts/conflicts/benefits, and 47% of the studies that used community engagement integrated other methods (Appendix S1). The species with the most community engagement studies was the spotted hyaena ($n = 80$). Of the studies employing community engagement, 57% ($n = 16$) of striped hyaena studies, 45% ($n = 5$) of brown hyaena studies, 45% ($n = 36$) of spotted hyaena studies and 0 aardwolf studies complemented community engagement with other methods. Direct observation of wildlife ($n=24$, 22%), tracks ($n=16$, 15%) and scat sampling ($n=15$, 14%) were the most common methods used alongside community engagement.

DISCUSSION

Geographic, temporal and topical trends in Hyaenidae literature

Overall, like many other scientific topics, annual research on the four species of Hyaenidae has increased exponentially since the first study was published on spotted hyaena in 1939 (Matthews 1939). There is a wide breadth of topics covered across the four species, yet there are strong geographical, species and topical biases within the body of existing research, and relatively few studies on human–hyaena interactions or anthropogenic impacts on the species. Nearly 50% of the studies took place in three countries: Kenya, South Africa and Tanzania. This is likely due to the long-running research projects on hyaenas in these three countries, which may simultaneously contribute to topical biases. As far as species biases, spotted hyaena dominate the literature while aardwolves are understudied. Although striped hyaena were historically among the least studied of the four species, there has been a recent burgeoning of striped hyaena research. Meanwhile, with 131 studies (14% of all hyaena studies), brown hyaena may be comparatively overrepresented in the literature given their relatively small range (five range states; Wiesel 2015).

TRENDS IN AARDWOLF RESEARCH

Despite comparatively few studies, aardwolf research has greatly contributed to our understanding of the evolution of insectivory in carnivorans (Westbury et al. 2021). However, we know little about aardwolf cognition or their ability to navigate novelty or human infrastructure, nor do we have any understanding of their role in and susceptibility to disease transmission. We thus lack clarity regarding the aardwolf's ability to adapt to novelty associated with changing land use such as expanding agriculture, increasing livestock densities and pastoralist sedentarization (Green 2015).

The relative lack of published research on aardwolves in relation to the larger hyaena species fits within a broader trend for small carnivores (Marneweck et al. 2021) and is likely further driven by the aardwolf's elusiveness and nocturnality (Williams et al. 1997, Spagnuolo et al. 2022). A lack of data on aardwolf distribution and population size across nearly all range countries, particularly in its north-eastern range, hampers conservation of the species, although a comprehensive update to the IUCN range maps and population estimates is underway (A. Jacobson and S.M. Dloniak, pers. comm.). There also remains the crucial question as to whether the southern and north-eastern populations of aardwolves are different subspecies, or even different species altogether (Koehler & Richardson 1990, Allio et al. 2021). This may have important implications for their conservation management, that is, if the two subspecies are on a pathway to speciation and have unique genetic diversity, then their respective preservation should be a priority. The aardwolf is currently classified as *Least Concern* by the IUCN, yet the paucity of research and data (67 published studies) raises the question of whether we know enough about aardwolves to make accurate decisions regarding their management.

TRENDS IN BROWN HYAENA RESEARCH

Studies on the brown hyaena showed the highest proportion of geographical coverage for any of the four species but this is likely due to the species only being found in five countries (Wiesel 2015). Nevertheless, these five range countries comprise nearly all of southern Africa. Research interest regarding the brown hyaena has grown over the last three decades and is principally driven by the interrelated questions of conservation status and anthropogenic threats (e.g. Grilo et al. 2021, Fischer et al. 2022). Many studies also take advantage of advancements in camera trap surveys to provide information on brown hyaena density (Welch & Parker 2016) and extent of occurrence (Williams et al. 2021), which helps to inform conservation management assessments.

Our knowledge of brown hyaena has benefited from long-term studies in open habitats that allow direct observation, such as projects in Namibia (Wiesel 2010), South Africa (Mills 1982) and Botswana (Owens & Owens 1978). However, some conclusions are likely context dependent and may not be representative of the species across their entire range. Recent publications are making advances in this regard by extracting 'by-catch' brown hyaena data from camera trapping studies that focus on other carnivores (Williams et al. 2021).

The ecology and diet of brown hyaena are also well studied, likely influenced by local investigations into the potential role of brown hyaena as livestock predators (Van der Merwe et al. 2009) and subsequent retaliation by landowners (St John et al. 2012). The extent of scavenging vs. predation of livestock has been quantified in protected areas via direct observation (Mills 1978) but has not been examined within unprotected areas. However, more recent ecological studies are providing evidence of the trophic roles that brown hyaena play in unprotected ecosystems (Kent & Hill 2013). Such studies improve upon our understanding of brown hyaena involvement in livestock depredations (Maude & Mills 2005) by examining the importance of scavenging opportunities for brown hyaena persistence (Yarnell et al. 2013). However, additional research is needed in unprotected ranch lands of southern Africa to understand the relative proportions of brown hyaena predation and scavenging (Faure et al. 2019) and thus aid in contextualizing livestock losses. Such research would complement the ongoing need to study brown hyaena more evenly across their range to identify whether their distribution is changing and which factors – both anthropogenic and ecological – may be limiting their range to southern Africa.

Other particularly well-studied aspects of brown hyaena research include their taxonomic status within the Hyaenidae (Westbury et al. 2021) and genetic population structure (Westbury et al. 2018) across their range, the latter of which shows low genetic diversity in relation to other extant carnivore species. Other publication topics were not well represented, including behaviour, disease, reproduction and human impacts, conflicts and benefits. This bias is likely due to this species being elusive and living at low densities (e.g. Rich et al. 2017), making it difficult to observe and study in the wild.

TRENDS IN SPOTTED HYAENA RESEARCH

The spotted hyaena was by far the most-studied species in our review, accounting for 75% of all publications. The relative political stability and infrastructure development in Kenya, Tanzania and South Africa likely play a role in the high representation of those countries for spotted hyaena studies. Kenya and Tanzania in particular host long-term field studies focused on free-ranging spotted hyaena in protected savannah ecosystems (see Hofer & East 1993, Holekamp & Dloniak 2010). Such study areas more readily allow for observing hyaenas directly during day and night and collecting detailed, long-term behavioural and demographic data. More recently, however, studies have begun to focus on spotted hyaena in challenging habitats (Braczkowski et al. 2022) where they are not as easy to directly observe or have not yet been studied (e.g. in the forests of the Congo Basin, mangrove and coastal areas in Senegal and other regions of West Africa, as well as montane areas of Ethiopia and Kenya). These will be important sites for future applied research that expands the breadth of knowledge on their ecology, behaviour and interactions with people in diverse, understudied ecosystems.

Spotted hyaena literature has largely focused on non-applied topics such as ecology and diet, endocrinology, anatomy, morphological development and behaviour and cognition. Such research has contributed immensely to the scientific understanding of mate choice, the evolution of intelligence, social behaviour and kin selection (e.g. Frank 1997, Smith et al. 2008). The spotted hyaena's unusual genitalia, individually unique pelage and hierarchical, female-dominated social system have made it an appealing model organism in behavioural and evolutionary ecology (Hofer & East 2003, Holekamp et al. 2007, Holekamp & Dloniak 2010). Similarly, its remarkable immune system and pathogen resistance have made the spotted hyaena the subject of a body of valuable research at the disease–ecology interface (East et al. 2001, Sonawane et al. 2021).

While basic research remains strongly represented in recent spotted hyaena literature, there is now a trend towards more management-focused research (Fig. 3), ostensibly to address the myriad interactions between spotted hyaena and people. Indeed, even within Kenya's protected Maasai Mara National Reserve, human-caused mortality has increased substantially over time (Pangle & Holekamp 2010). Generally, spotted hyaena are facing increasing levels of anthropogenic pressure both inside and outside of protected areas (Mills & Hofer 1998, Wilkinson et al. 2021b, Dheer et al. 2022). As the largest and most gregarious of the four species (Holekamp & Dloniak 2010, Holekamp et al. 2012), along with being the most widespread apex predator within Hyaenidae, the spotted hyaena experiences higher levels of both perceived and realized conflict with people. Thus, applied research across habitats and gradients of anthropogenic influence that builds upon findings within basic research topics will be crucial for the species' persistence.

TRENDS IN STRIPED HYAENA RESEARCH

While it had the second most studies, the striped hyaena was considerably less studied than the spotted hyaena, which could be attributed to the striped hyaena's typically smaller group sizes, its ability to persist at low densities and its nocturnal, elusive behaviour (Mills & Hofer 1998, Harihar et al. 2010). However, the striped hyaena distribution range is much wider than other hyaenids – spanning parts of South Asia, the Middle East and Africa (AbiSaid & Dloniak 2015). Notably, there have been very few studies from the Middle East, even though the Middle Eastern range states contribute to significant hyaena populations; for example, there are potentially >1000 individuals in Egypt alone and up to 1000 individuals each in Iraq and Saudi Arabia (Mills & Hofer 1998). The rugged terrain in which striped hyaena often reside in these range states, along with security challenges in many of its range states, likely contributes to this geographical bias (Dudley et al. 2002). Possibly related to these logistical difficulties, publications on striped hyaena focus broadly on population and range by using camera traps or landscape-scale models, while only a few studies focus on fine-scale individual behaviour using GPS/VHF collars or direct observations (Wagner 2006, Califf et al. 2020, Bar-Ziv et al. 2022).

Ecology and diet and human impacts, conflicts and benefits were other major foci within striped hyaena literature, likely due to increasing interactions or shared spaces between people and striped hyaena (Panda et al. 2022). Striped hyaena are attracted to scavenging from available anthropogenic food sources in human-dominated areas (AbiSaid & Dloniak 2015). Thus, a combination of reduced habitat and prey availability, along with an affinity for anthropogenic attractants, can result in conflicts with striped hyaena (Mills & Hofer 1998, Bhandari et al. 2021). As striped hyaena continue to be reported in new locations (Akash et al. 2021, Bhandari et al. 2021, Çoğal et al. 2021) outside of protected areas, and as human–hyaena spatial overlap increases, more research on human perspectives towards striped hyaena and fine-scale striped hyaena behaviour may foster coexistence.

Management, conservation and threats

While research has generally begun to shift towards increasing studies on human impacts, conflicts and benefits, these topics still have a species bias, and we also have a limited understanding of both natural and anthropogenic mortality. For comparison, the leopard (*Panthera pardus*) occupies a similar percentage (to spotted hyaena) of its historical range (Ripple et al. 2014), yet a Web of Science search on studies regarding leopard conservation from 2010 to 2022 yields nearly 500 results – nearly double that of all conservation-related studies on *all* Hyaenidae during the same period. Notably, most studies regarding people were oriented around human–hyaena interactions and conflicts, and tended to involve livestock-related conflict – particularly for spotted and striped hyaena. Except for more tolerant regions of Ethiopia, which have religious connections to and in some cases receive ecotourism benefits from spotted hyaena (Yirga et al. 2013), livestock-related interactions contribute to negative perceptions that may impact hyaena populations and species that are uninvolved in conflict (Green 2015, Wiesel 2015).

Indeed, both realized and perceived human–carnivore conflicts (Wilkinson et al. 2021a) are politically rife and can have cascading effects on people (e.g. through economic losses; Yirga et al. 2013) and carnivores. For example, conservation NGOs have granted funds that have resulted in the culling of spotted hyaena ostensibly to minimize hyaena attacks on humans (e.g. Hersi 2008). Regarding perceived conflicts, communities have also been known to persecute hyaenas without a specific link to a livestock predation event (Kissui 2008). Despite the clear importance of community engagement in effective hyaena management and conservation, few Hyaenidae studies incorporated interviews and traditional ecological knowledge into their methods. Valuing meaningful community engagement in wildlife research can be critical for gaining more holistic understanding of ecology (Moller et al. 2004, Trisos et al. 2021) and for anticipating and mitigating challenges that communities face in relation to local wildlife and ecosystems (Hosen et al. 2020, Taremwa et al. 2021). In the face of anthropogenic change and increasing human–hyaena interactions, integrating local community attitudes, values and perceptions into study methods (e.g. Ceaușu et al. 2018, Ostermann-Miyashita et al. 2021) will be essential for current and future hyaena management. Community engagement will also be key to addressing the paucity in our understanding of the effectiveness of human–hyaena conflict interventions across social-ecological contexts (see Van Eeden et al. 2018, Lozano et al. 2019, Wilkinson et al. 2021a).

PROTECTED AREA STATUS AND DIET

Overall, most studies on Hyaenidae took place inside of protected areas, despite protected areas comprising less than 5% of the distribution range of all four hyaena species. Across species, the disproportionate focus on research within protected areas is likely to be obscuring important avenues of research and management that could be exclusive to or exacerbated within unprotected areas. Only one-fifth of the studies within protected areas concerned human impacts, while nearly two-thirds of studies that occurred exclusively outside of protected areas concerned human impacts, conflicts and benefits. If management is a priority for Hyaenidae, as we argue, then there is a clear need for more research outside of protected areas.

While it is critical to conduct research outside of protected areas that is specifically focused on anthropogenic impacts and human–hyaena interactions, it is also important to study basic hyaena behaviour, ecology and biology in unprotected areas to better determine and contextualize hyaena abilities to persist in human-dominated landscapes (see Pangle & Holekamp 2010, Di Minin et al. 2016). For example, research on striped hyaena has been disproportionately conducted in unprotected areas, and this species also had the highest proportion of studies focused on human impacts, conflicts and benefits. Yet, for both spotted and striped hyaena, evidence points to their behavioural plasticity aiding them in surviving outside of protected areas without necessarily engaging in or experiencing negative human–hyaena interactions (Yirga et al. 2013, Panda et al. 2022). However, all four hyaena species had at least one record of eating anthropogenically derived foods, particularly livestock, game and – rarely but present in all species – human refuse or even human remains (Appendix S1). More than two-thirds of diet records for striped hyaena included livestock, and livestock appeared in more than a third of spotted and brown hyaena diet records. For many of these records, it was unknown whether livestock were hunted or scavenged (Maude & Mills 2005, Yirga et al. 2015), and we also know that some communities are tolerant or even welcoming of such scavenging (Yirga et al. 2013), although this is not the norm. Yet human–hyaena conflicts, and perceptions thereof, continue to contribute towards overwhelmingly negative attitudes regarding Hyaenidae (Macdonald et al. 2022).

MORTALITY

Regarding threats to the Hyaenidae, fewer than 10% of our examined studies investigated mortality causes and intensity, and there are very few long-term and contextual studies assessing the subject. Even the available long-term data were often collected as bycatch of other research projects, or with a specific focus, such as disease monitoring or human–wildlife conflict (Begg et al. 2007, Höner et al. 2012). There is thus a need for robust research investigating the relative frequency of mortality sources in relation to other factors such as population size. Understanding the extent of and interactions between anthropogenic and non-anthropogenic mortality causes will improve targeted and effective conservation management measures for hyaenas (Cardillo et al. 2004, Collins & Kays 2011). To address the mortality research gap, we recommend investing in long-term hyaena research projects in unprotected areas, using increasingly affordable tools (such as camera traps) as well as reports from community scientists, and providing avenues for reporting of 'bycatch' about hyaena populations and mortality from non-hyaena studies.

An added concern across all hyaena species is the bias towards reporting anthropogenic mortality. Anecdotal records, for instance, are commonly comprised of anthropogenic mortality sources, such as those caused by vehicle collisions or conflicts with livestock farmers. However, these causes may be disproportionately reported due to their relevance to humans, increased visibility or perceived unusualness. In an analysis of terrestrial mammal mortality in North America, vehicle collisions and intentional human-caused killings were also reported most frequently (Collins & Kays 2011). Comprehensive contextual studies assessing all mortality causes, both inside and outside of protected areas, are needed to clarify the relative burden of anthropogenic threats towards hyaenas and determine whether they are additive to natural mortality and threaten population viability (e.g. as in the case of mountain lions [*Puma concolor*], Benson et al. 2023), and thus better inform future management strategies.

Lastly, there is a lack of studies investigating natural mortality causes outside of protected areas. Notably, even within protected areas where there should be less human–hyaena conflict, there are more records of anthropogenic compared to natural causes (Fig. 6a). In contrast, analyses of leopard mortality in protected vs. unprotected areas show a prevalence of natural mortality events inside protected areas, while anthropogenic causes dominate mortalities outside of protected areas (Swanepoel et al. 2015). This either suggests that the beneficial effect of protected area status for reducing carnivore mortality (Adhikari et al. 2022) differs for hyaena species, or it further indicates overreporting of human-induced mortality.

Implications for future research

Despite the ecological importance of hyaena species and their myriad interactions with people, compared to human–felid and human–large herbivore conflicts (Panthera.org, Tensen 2018, Conley 2019, Schaffer et al. 2019, Eikelboom et al. 2020) very little funding and effort has gone towards resolving human–hyaena conflict through research, conservation management initiatives and other mitigation. For example, of the >7500 grant applications regarding mammal species to the Mohammed bin Zayed Species Conservation Fund (MBZ), an endowment that promotes species conservation, only 7 have listed 'hyaena' as a focal species. A lack of funding could be the primary driver of the relative lack of research on human impacts and human–hyaena interactions. The unique ecological roles of the Hyaenidae and their varied relationships with people across their range merit viewing research on their specific conservation management as paramount, aligned with the axiom of 'keeping common species common' (Frimpong 2018), which interrelates with the importance of large carnivores as biodiversity indicators (Natsukawa & Sergio 2022). Because of their wide geographic ranges and social-ecological contexts, we propose that hyaena could also serve as model species for wildlife conservation management – as they already are for behavioural ecology – such that research and practice regarding hyaena management could guide practitioners across contexts in understanding and providing solutions to human–wildlife conflicts, stemming losses of large carnivores and implementing lasting mechanisms for interdisciplinarity and inclusivity.

CONCLUSIONS

With increasing anthropogenic impacts such as climate change, habitat degradation and loss and persecution of carnivores (Ripple et al. 2014), there remains much room for innovative research on the threats to the Hyaenidae, the effects of hyaena species on human livelihoods and best practices for their conservation management. Additionally, with much of their range occurring outside of protected areas, we have a particularly urgent need to address gaps in foundational knowledge of these species' ecology and behaviour in human-dominated landscapes. Because of the myriad interactions between humans and hyaena species worldwide, we recommend research and management practices that bolster community engagement and elevate traditional ecological knowledge to more holistically understand how hyaena species may survive, thrive and coexist with people going forward into the 21st century.

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AUTHOR CONTRIBUTIONS

Conceptualization: C.E.W. and A.D.; Methodology: C.E.W. and T.Z.; Investigation: C.E.W., A.D., T.Z., S.B., M.T.-T. and E.B.Z.; Writing – Original Draft: C.E.W., A.D., T.Z., S.B., M.T.-T., E.B.Z., R.W.Y. and A.J.; Writing – Review & Editing: C.E.W., A.D., M.T.-T., A.J., R.W.Y and S.M.D.

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DATA AVAILABILITY STATEMENT

Data availability is not applicable to this article as no new data were generated. Additional reference lists used for the review are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Includes literature review search terms, detailed geographical and topical summaries, all estimates and odds ratios from loglinear models, mortality analysis categories and summaries, visualization of interdisciplinary topics and methods and visualization of correlation plots from chi-square analyses.