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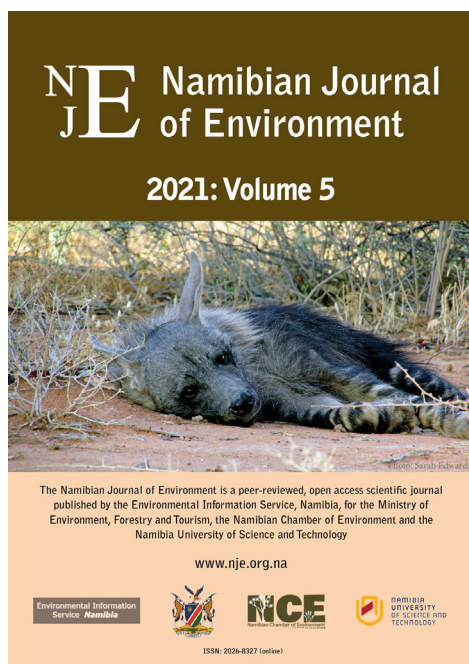
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SECTION A: RESEARCH ARTICLES

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Of teeth and claws: Taking stock of carnivore research in the greater Etosha landscape

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ABSTRACT

The Etosha National Park and its surrounding areas in northern Namibia have been the focus of research for more than a century, yielding a great amount of environmental and ecological knowledge. The results have appeared in different forms and formats, and these are stored in numerous repositories, many of which are difficult to access. This limits distribution and effective use of existing knowledge about specific topics and biological taxa, whilst also constraining the opportunity to identify future research priorities. In this study, we assessed published and unpublished accounts to compile an overview of previous mammalian carnivore research in the greater Etosha landscape – one of the few remaining large sub-Saharan areas (> 69,000 km²) with a nearly intact carnivore guild. Of the 644 carnivore-related documents we found, 139 studies met our inclusion criteria. From these, we identified trends emerging from spatial, temporal, species, authorship, and topic patterns, whilst also digitising source materials and creating an annotated bibliography that is being made available to others. Our synthesis of carnivore research revealed several historical biases in terms of: i) where carnivore studies occurred (mainly within National Park boundaries); ii) which species were studied (mostly large-bodied, charismatic animals, especially the lion *Panthera leo*); and iii) which research themes and topics prevailed (mostly ecology topics focussing on occurrence, diet, and demographics). We also found that carnivore research output has been declining during the last three decades and this was accompanied by a shift in lead authorship from government-employed researchers to external investigators. We use our results to provide a stimulus for re-focusing future carnivore studies. We encourage similar syntheses and stock-taking of what is known for other taxa and topic areas, stressing the importance of preserving historical knowledge and making it accessible.

Keywords: bibliography; Carnivora; Etosha National Park; Namibia; predator; protected area; research history; synthesis

INTRODUCTION

The Etosha National Park (hereafter ENP) in northern Namibia is an example of a large African conservation area with a long and well documented history in research and monitoring. For nearly six decades, numerous studies covering a wide range of topics have been conducted in and around ENP. Fields of study have included, among many others, the measuring of soil and water characteristics, surveys to estimate animal numbers, wildlife natural history, rainfall patterns, disease investigations, and factors affecting large animal movement patterns. Most of the resulting data, stored as hard copies at the Etosha Ecological Institute (hereafter EEI), were either compiled as internal reports, peer-reviewed publications, book chapters, academic theses, or conference proceedings.

The EEI, which opened on 1 April 1974 (Berry 1997), is responsible for securing and disseminating scientific data generated in ENP. Since the inception of the EEI, a large amount of information has been collected and substantial technological advances made to improve data collection, analyses, and interpretation. This assisted science-based decision-

making in ENP. However, unless a centralised data repository for the safe storage, management and dissemination of all current and historic data is established, there is a risk of losing a wealth of institutional knowledge due to generation overturn among researchers and changes in knowledge distribution technologies and formats. In addition, the availability of historic knowledge is often constrained by inaccessible data repositories or incompatible formats, which can be difficult and time-consuming to reconcile and standardise in digital format. The latter is a prerequisite for accessing and distributing knowledge on a global scale.

Mammalian carnivores are the focus of extensive research across the world, mainly because their importance in ecosystem functioning is increasingly recognised (Ripple *et al.* 2014). The greater Etosha landscape is no exception, and structured carnivore research began as early as the mid-1960s, with the first published report assessing the population sizes of lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), and (Cape) wild cat (*Felis lybica/silvestris*) in 1972 (Reid 1972). In addition, this landscape provides a representative example of global conservation

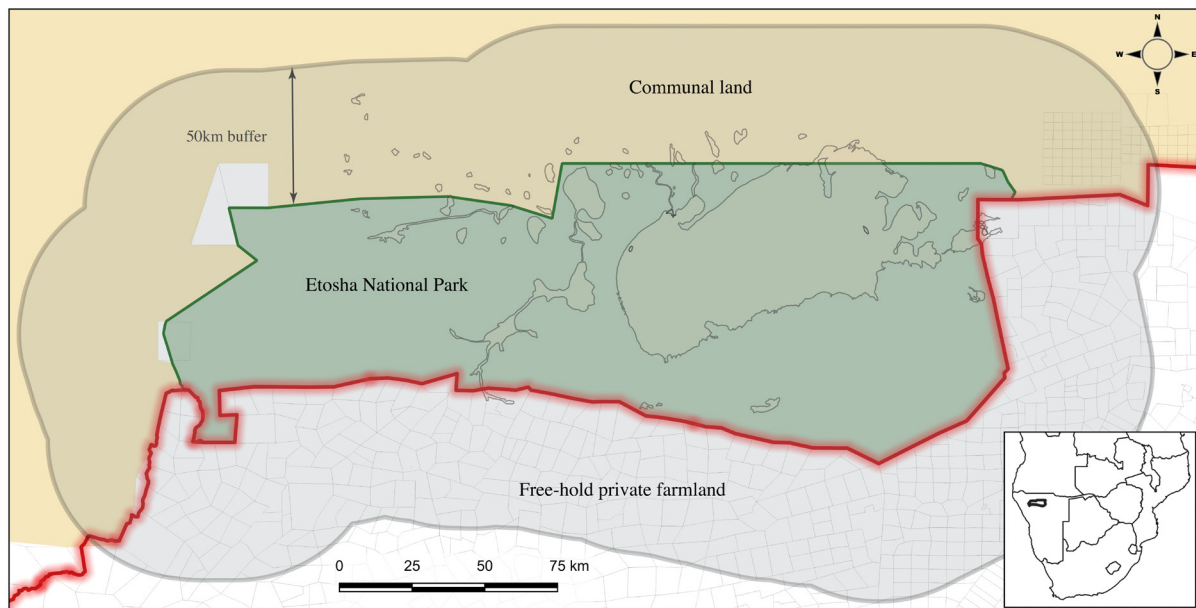


Figure 1: Extent of the carnivore research study area in northern-central Namibia. Our focal area encompassed 69,092 km², including 23,163 km² of free-hold, multi-use farmland, the state-protected Etosha National Park measuring 22,904 km², and 23,025 km² of multi-use communal lands. The red line shows the veterinary cordon fence. The inset shows the focal area's location in the southern African sub-region.

challenges, with a core protected area surrounded by a matrix of human multiple-use systems. It is internationally recognised as one of the last conservation areas in sub-Saharan Africa with a largely intact predator guild (Wolf & Ripple 2017). Despite the local extinction of African wild dogs (*Lycaon pictus*) in the 1980s, ENP still supports source populations of five large carnivore species, including lion, leopard (*Panthera pardus*), cheetah, spotted hyaena (*Crocuta crocuta*) and brown hyaena (*Parahyaena brunnea*), as well as an associated range of medium-sized meso-carnivores. This provides a rare opportunity to study functional guilds and trophic interactions between predators and their prey populations.

Our goal was to write an overview paper, with a focus on the mammalian carnivore guild occurring in the greater Etosha landscape, whilst also creating an annotated bibliography and making materials available to others as a digital library. Our motivation to conduct this work stemmed from the global importance of long-term carnivore research and conservation, as well as the availability of numerous publications and unpublished reports. The value and impact of similar reviews was illustrated by Balme *et al.* (2014), in their paper on drivers determining priorities for leopard research and conservation.

We structured our work as a synthesis of available materials, with the intention of summarising and condensing existing information, identifying patterns and trends, and highlighting research gaps to stimulate future studies.

METHODS

Scope

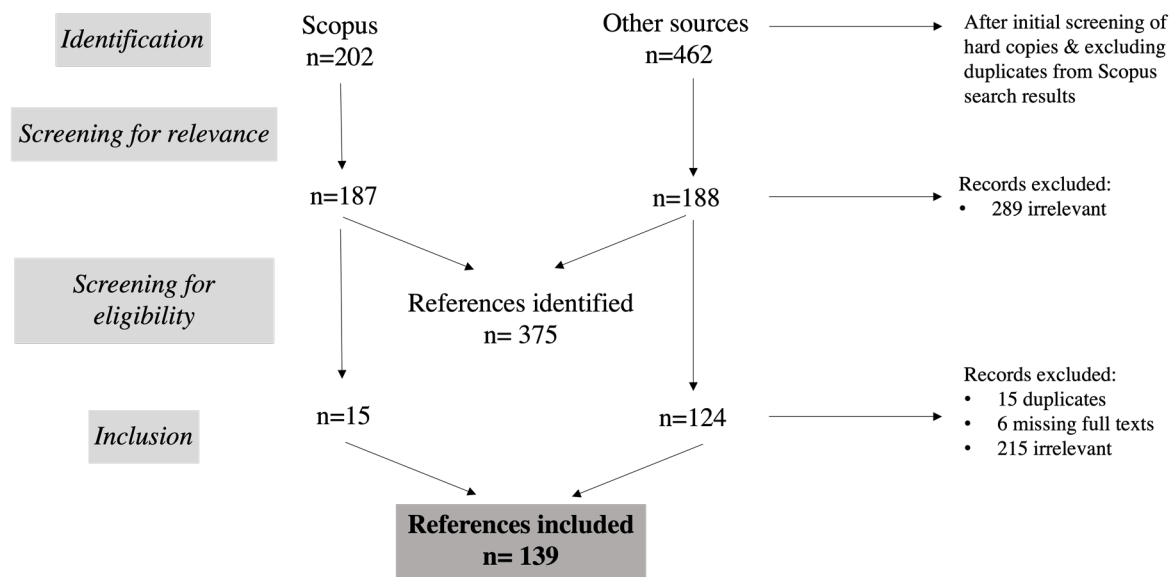
The focal area was defined as the greater Etosha landscape in northern Namibia, including the ENP and an arbitrarily defined 50 km buffer around its current boundaries (Figure 1). This 69,092 km² landscape encompasses three main land tenure system at nearly equal area proportions, being: 23,163 km² of free-hold, multi-use farmland to the South and East of ENP, the state-protected ENP of 22,904 km² in its centre, and 23,025 km² of communal, multi-use residential and farmland to the West and North of ENP (Figure 1). Any historical carnivore research in this area, even if only partly overlapping with it, was considered for inclusion.

Sayer (2018) emphasised the aim of considering the entire historic account of literature. Hence, we had no temporal exclusion rule, assessing documents published during the last 110 years, with contents dating as far back as the 19th century. Our synthesis focussed on large-bodied mammalian carnivores, including lion, leopard, cheetah, spotted hyaena, brown hyaena and African wild dog as well as medium-sized carnivores, including honey badger (*Mellivora capensis*), black-backed jackal (*Canis/Lupulella mesomelas*), serval (*Leptailurus serval*), and caracal (*Caracal caracal*). In our search, we considered species' Latin names, their vernacular names and common synonyms, and also spelling variants in different languages (Appendix 1), including documents in English, German and Afrikaans.

Material sources

Materials were retrieved through structured searches from a broad spectrum of published and unpublished sources, whilst also obtaining materials opportunistically, for example from research colleagues. Structured carnivore literature searches were carried out between April and October 2020. First, we conducted a detailed abstract, title and keywords search using the SCOPUS online database on 16th April 2020. Our primary search terms included: “hyaena/hyena”, “lion”, “leopard”, “cheetah”, “wild dog”, “badger”, “jackal”, “serval”,

and “caracal” and each of these was paired with the secondary search term “Namibia”. In addition, we browsed the entire holdings of Etosha Ecological Institute’s research archives, manually extracting relevant files. We also searched for materials in Google Scholar, the open online repository of Namibia’s Environmental Information Service (www.the-eis.com) and the Digital Cat Library of the IUCN/SCC Cat Specialist Group (<http://www.catsg.org/catsglib/index.php>). Full publications lists of Namibia’s research titles: Madoqua, Roan News, Cimbebasia (journal of the State Museum, Windhoek) and Mitteilungen der Wissenschaftlichen



Journal articles	15	55
Magazine	-	2
Newspaper	-	1
Presentations	-	3
Reports	-	49
Thesis	-	7

	Applied research	Ecological research	Method development	TOTAL*
PA	33	92	21	117
Free-hold private farmland	22	34	6	47
Communal land	13	16	1	23
TOTAL*	44	107	21	139

* The total number of studies for themes and location differ from the overall number of studies assessed, as each reference could qualify for multiple themes and locations.

Figure 2: Flowchart outlining the source material review and selection process, including the distribution of eligible references in terms of reference type, research type, and study location. Out of 664 carnivore-related documents initially identified, 139 references were included in the synthesis. Most references were peer-reviewed journal articles (50.4%) and reports (35.4%). The majority of research was conducted within Etosha National Park (84.2%) and focussed on ecology topics (77.0%). [Appendix 2](#) and [Appendix 3](#) provide the full account of references included and six items for which full texts were not accessible.

Gesellschaft (Namibia Scientific Society's periodical newsletter) were screened, as well as de Waal's (2002) large predator bibliography and the bibliography of the Northern Namibian Environmental Project (Ministry of Environment and Tourism in Namibia 1997). Finally, we conducted a tri-lingual abstract, title and keyword search of the library holdings of the Namibia Scientific Society (<https://www.namscience.com/library>). Search terminology was consistent across all sources.

We considered any document format, digital and print, including peer-reviewed research articles, book chapters, academic theses, grey reports, policy documents, unpublished research reports, conference proceedings, presentations, posters etc. Since we were primarily interested in compiling a bibliographical overview of previous scientific studies, only materials with an obvious research element, those containing original data and an analysis thereof, be they descriptive and/or inferential, were considered. We excluded popular science articles or news materials that only described studies and/or their results. To avoid pseudo-replication, we removed duplicate publications of the same studies and assessed the contents of sequential documents (e.g., interim project progress reports), in both cases only including the most comprehensive study account in our review, usually the latest or final version, though not always ($n = 2$). Raw data

accounts as well as documents only containing general correspondence about research projects, project proposals, meeting minutes, and any other documents not providing original data and some form of formal analysis thereof, were rejected. Figure 2 outlines the literature search and selection process, including sample sizes and general results.

Processing and analysis

For processing and future reference, all relevant materials were digitised, imported into a Zotero literature database (<https://www.zotero.org>), from which we created an annotated bibliography in Excel format that contains publication and content details, as well as the source of materials. For each document matching our search criteria, we read the full account and, if also matching our inclusion criteria, the following information was extracted: author(s) and document title, year of publication, publication title, volume and issue, page numbers, DOI, and source URL. We categorised studies by type of publication such as *peer-reviewed journal article*, *report*, *academic thesis*, *book chapter*, *poster*, *conference paper*, *presentation*, and *magazine/newspaper article* and also by broad theme, being: *applied research*, *ecological research* or *methods research* (Table 1). Based on the study's specific objectives and the data and analyses contained, materials were categorised by study focus and specific topic (Table 1). Neither

Table 1: Study themes and specific topics used for literature categorisation.

Broad theme	Examples of data contained, or analyses performed
Applied research	Management investigations, e.g., translocations, population control measures, human-carnivore conflict topics
Ecological research	Natural history investigations, e.g., population demographics or spatial ecology studies
Methods research	Methodology studies involving carnivores as experimental units, e.g., development of immobilisation procedures
Study topic/focus	
Distribution	Presence-absence and occurrence surveys
Population	Abundance, density, population trends
Demographics	Group size, group composition, sex ratios, age classes
Mortality	Numbers and causes
Physiology	Organism and body part functioning
Reproduction	Litter size, gestation period, birth interval
Feeding ecology	Diet composition, preferences, hunting
Spatial ecology	Home range size, movements, habitat selection
Behaviour	Communication, activity budgets, behaviour patterns
Interactions	Inter- and intra-specific interactions
Genetics	Genetic relatedness, population genetics, heredity
Disease	Parasites, pathogens, clinical manifestation
Human-carnivore interactions	Conflict, tourism, fences, trophy hunting, utilisation
Management	Population control, translocation, policies
Immobilisation/Anaesthesia	Darting and restraint methods, testing of immobilisation technology and chemicals
Other	Any other contents not fitting the above categories

broad themes nor specific topics were mutually exclusive. In case of any uncertainty during literature categorisation, we used a double-observer rule for theme and content decisions.

For each reference, we extracted information about the focal species, the year(s) of data collection, geographic details, land tenure and land use information provided for the study area, as well as the specific data contained, such as any empirical information presented about carnivore group size, group composition, home range size etc. (Table 1). Finally, each document's reference list/bibliography was scanned to identify additional research items of interest.

We summarised results by the number of relevant, non-duplicate references (i.e., unique research items), rather than by the number of original studies because several long-term studies resulted in multiple publications with different study foci, results, and analyses. Furthermore, some publications contained cross-sections of the data and results obtained from multiple studies. We employed mainly descriptive statistics to analyse spatial, temporal, authorship and content patterns and trends. Since data categories were not mutually exclusive, for example a study being carried out across more than one land tenure category, the sum of relative proportions presented may exceed 100%. Results were temporally binned by decade, using the year(s) of data collection for categorisation, as opposed to publication date. Studies that spanned multiple decades were included in each. We sourced average adult female body mass estimates of the focal species from Skinner and Chimbimba (2005) and Estes (1991) using estimates from study sites nearest to ENP. We processed and analysed data with Microsoft Excel, JMP Pro v15 (SAS Institute Inc. 2020) and R v4.0.2 (R Core Team 2020).

RESULTS

Overview: effort and valuable references

Our initial search yielded 664 carnivore-related documents for assessment, of which 375 were screened for eligibility. A total of 139 (37.1%) documents met the selection criteria and were included in the synthesis (Figure 2, [Appendix 2](#) and [Appendix 3](#)). As a key product of this work, we created a digital, annotated bibliography of the final 139 references ([Appendix 2](#)), containing publication details as well as the information on broad study themes and specific topics, the focal species studied, study duration, and study area. Since about half of all full texts are not freely available online ($n = 70$; 50.4%), the bibliography also contains details of where these items can be sourced.

We found 13 references (9.4%) that were included but reported insufficient detail on the dates of data collection. Similarly, 49 references (35.3%) reported only a vague description of the study area such as “*Etosha National Park*”, without providing further detail on specific locations or sample origin. One reference reported results for “*hyaena*”, without providing clarity which species was studied. This reference was, therefore, excluded from species-specific analyses. Except for two references (1.4%) that were published in German, all materials included in the final analyses were published in English. In addition to focusing on at least one of our ten species of interest, three references also presented results on aardwolf (*Proteles cristata*), and one reference bat-eared fox (*Otocyon megalotis*), Cape fox (*Vulpes chama*), and African wild cat (*Felis silvestris*), respectively.

Temporal distribution and authorship

The carnivore documents we assessed dated back into the 1910s, with some reported contents extending into the late 19th century. However, structured carnivore research in the greater Etosha landscape only commenced during the second half of the 20th century (Figure 2). We found a clear increase in research output beginning in the 1960s, with a peak in the 1980s, followed by a subsequent decline from the 1990s until present (Figures 3a and 3b). There were 21 references (15.1%) reporting research results based on data collected for 10 years or longer, predominantly during the 1960s-1990s. A total of 288 authors contributed to the 139 references, with ENP staff Philip Stander ($n = 23$, 16.5%) and Hu Berry ($n = 15$, 10.8%) contributing to most references overall. Another three independent researchers each contributed to 8-11 references respectively, equivalent of > 5% of all references. The majority of authors ($n = 258$, 89.6%) contributed to one or two references. Overall, first authorship was approximately even between government employees ($n = 66$, 47.5%) and external researchers ($n = 71$, 51.1%) but relative contributions varied strongly over time (Figure 3a). Whilst first authorship could not be ascertained for two items (1.4%), government-employed researchers (Ministry of Environment, Forestry and Tourism including EEI staff) led carnivore publications for three decades (1960s-1980s). This trend reversed post-independence (1991) with external researchers gradually replacing them as lead authors, and most recently appearing as first authors on > 90% carnivore references (Figure 3a). Of the 139 references, 72 (51.8%) were peer-reviewed research articles and book chapters, 61 were grey literature (43.9%), whilst the remaining six (4.3%) were academic theses (Figure 3b). The latter contributed least to overall research output in terms of absolute numbers, but not necessarily in terms of the knowledge gained.

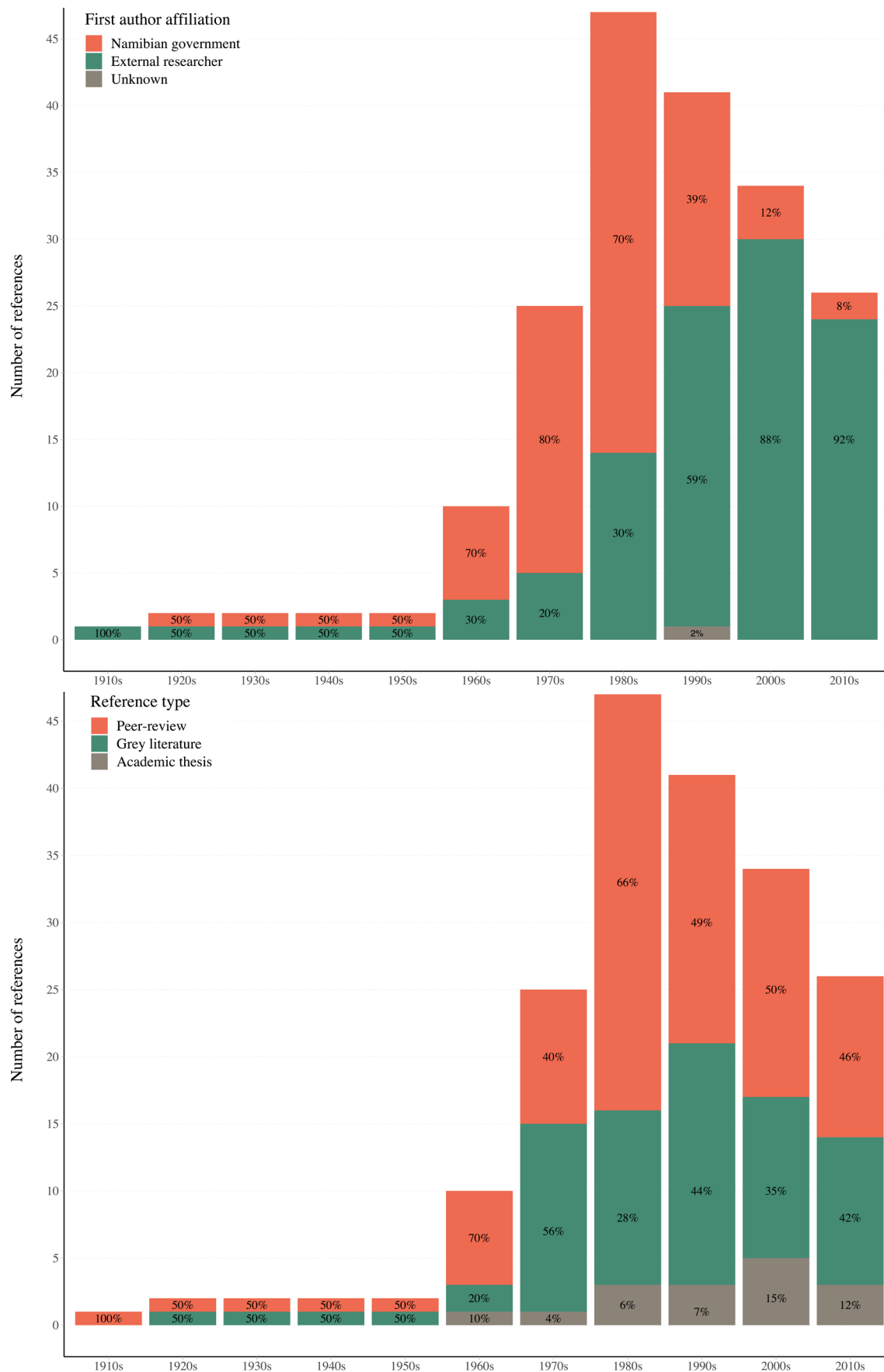


Figure 3: Temporal distribution of research reference first author affiliations between 1910 and 2010 (3a; top) and reference types during the same period (3b; bottom). The results demonstrate an increasing trend in carnivore research between the 1960s and 1990s, with a peak in the 1980s and a subsequent decline until present. The leading role of Namibian government researchers in carnivore publications reversed post-independence, gradually being replaced by external researchers (3b). Academic studies became more prevalent since the 1980s, coinciding with a substantial and continuous decrease in peer-reviewed publications and growing contribution of grey literature publication formats (3b).

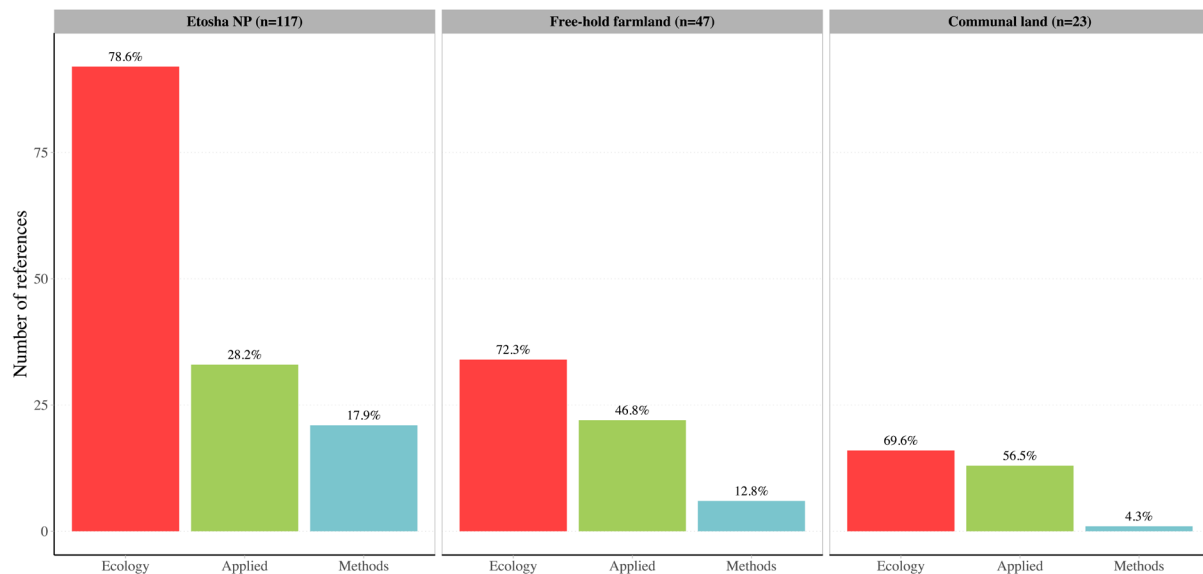


Figure 4: Graph showing the relative contribution of different study themes to all publications across the three main land tenure systems. Proportions reveal a clear prevalence of ecology studies across all land tenures and a strong overall bias toward studies being carried out in Etosha NP. Theme categories were not mutually exclusive; each reference could qualify for multiple categories. Thus, the sum of relative proportions may exceed 100%.

Spatial distribution and research themes

Although the three main land tenure systems contributed to the focus area almost equally in terms of area (Figure 1), there was a significant bias ($\chi^2 = 77.268$, $p < 0.00001$) toward carnivore research inside ENP ($n = 117$, 84.2%), followed by private, free-hold farmland references ($n = 47$, 33.8%), and lastly communal lands ($n = 23$, 16.5%, Figure 2 & 4). The bias toward the protected area held true for all ten focal carnivore species (Figure 5). Irrespective of land tenure, there was also a clear, significant bias in terms of broad research themes ($\chi^2 = 67.098$, $p < 0.00001$), with references predominantly comprising of ecology studies ($n = 107$, 77.0%), whereas only 44 references (31.7%) contained a focus on applied carnivore management, and 21 references (15.1%) included a methods component (Figures 2 & 4). Ecology was the dominant broad theme for any of the focal species, with a minimum relative contribution of 66.7% for caracal and, in some cases featuring as a focus in 100% of references (for serval and honey badger, Figure 5). Conversely, methods references consistently had the lowest contribution to research output per species ($< 10\%$) and four species (brown hyaena, honey badger, caracal, and serval) had no references entailing a methods development component (Figure 5). Most references ($n = 110$, 79.1%) dealt with a single research theme, whilst 25 references (18.0%) had a dual theme focus, and four references (2.9%) covered all three research themes. Influenced by several human-carnivore conflict studies outside ENP, the relative proportion of applied management studies was considerably higher on private, free-hold farmlands (46.8%) and highest

in communal lands (56.5%, Figure 4). Methods studies predominantly occurred in ENP (Figure 4), with a particular focus on lion and African wild dog (Figure 5), and mainly including population control via contraception (lion) and the development of chemical immobilisation procedures. Methods references had a higher relative contribution on private, free-hold farmlands when compared with communal areas (Figure 4). Large-bodied carnivores generally had a higher proportion of applied studies, although this was not apparent for the spotted hyaena (Figure 5). Caracal and black-backed jackal had the highest proportions of applied references amongst the medium-sized carnivores.

Species and study topics

There was a strong bias in terms of species coverage in carnivore research (Figure 6). Overall, the majority of references ($n = 97$, 69.8%) focussed on a single species only, 11 references (7.9%) focussed on two species, and 31 (22.3%) focussed on three or more species simultaneously. The most common combination of any two species was lion-spotted hyaena ($n = 29$, Appendix 2). Research predominantly focussed on large-bodied carnivores, with at least one of the six species featuring as the focal species in 128 (92.1%) of all references (Appendix 2). A Spearman's rank correlation analysis revealed a significant association between species' average adult female body mass and relative contribution to all references ($S = 61.686$, $R_{ho} = 0.626$, $p = 0.0263$, $n = 10$), suggesting that research focus was indeed biased toward the larger, charismatic species. This bias was mainly driven by

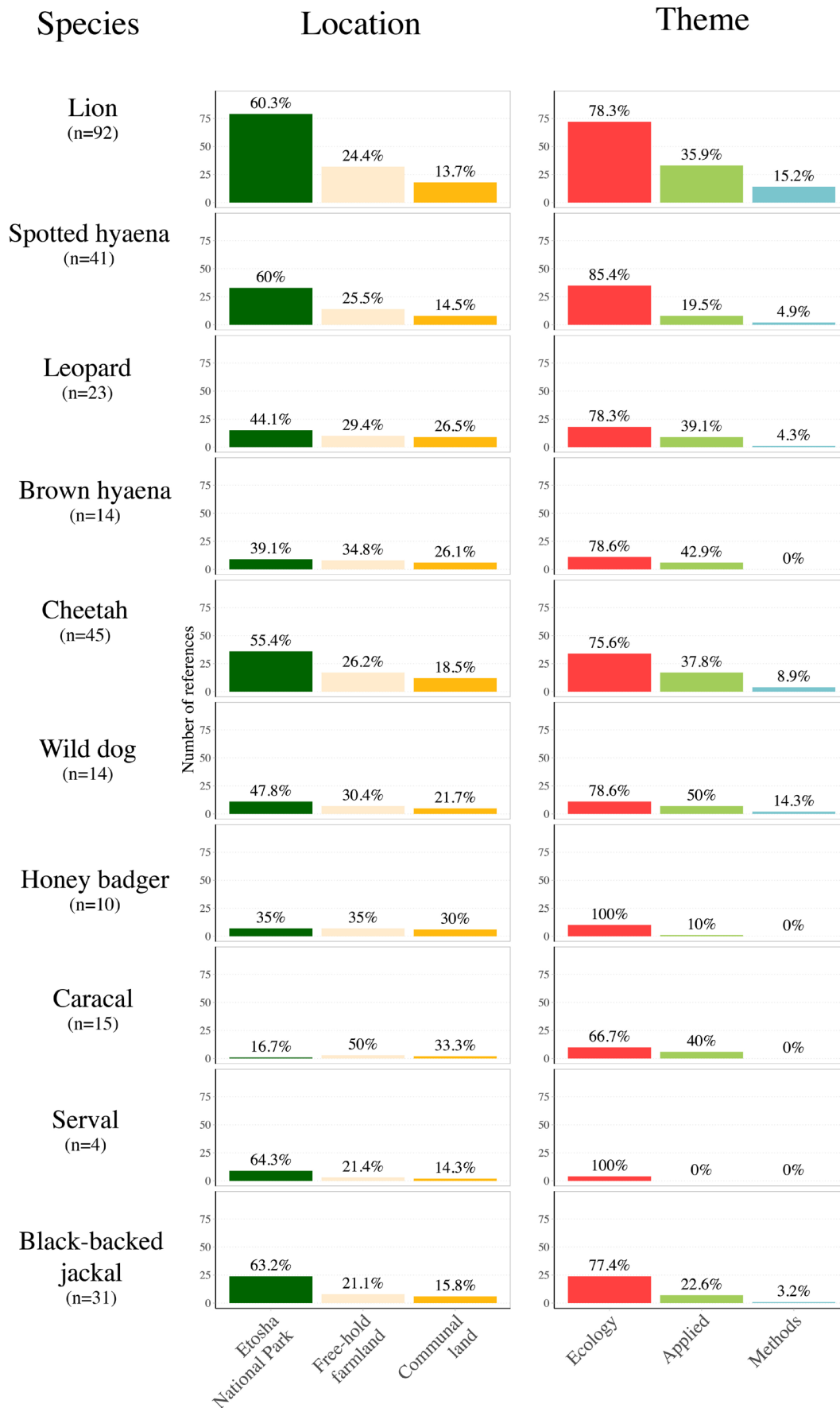


Figure 5: Relative proportions of references for the three main study themes and different land tenures for each carnivore species. Panels are scaled to the number of references. Neither broad research theme nor land tenure categories were mutually exclusive and, thus, the sum of relative proportions may exceed 100%.

a strong research focus on lion, which was a focal species in 92 references (66.2%), thus featuring more than twice as often as any other carnivore, followed by cheetah ($n = 45$, 32.4%), and spotted hyaena ($n = 41$, 29.5%, Figure 5). Of the larger carnivores, brown hyaena and African wild dog were least studied, with 14 references each (10.1%, Figure 5). The most commonly studied medium-sized carnivore, and fourth most studied species overall, was black-backed jackal with a total of 31 references (22.3%, Figure 5). The other six species each featured in $< 17\%$ of references, with serval having the lowest representation of 2.9% ($n = 4$). Other medium-sized carnivores, such as caracal and honey badger, only appeared in 15 references (10.8%) or less (Figure 5).

We identified 15 main topics in the carnivore research literature (Table 1) and 52 references (37.4%) focussed on a single research topic, 43

(30.9%) contained two topics, 19 (13.7%) covered three topics simultaneously, with the remainder of references ($n = 25$, 18.0%) addressing four topics or more. Lion, cheetah, and spotted hyaena were the only species with references containing results on all topics, and despite its current absence from the region of interest, African wild dog references covered all topics but one (i.e., reproduction, Figure 6). Our species-topic matrix revealed largest research gaps for leopard and brown hyaena as well as the four medium-sized species, of which black-backed jackal had the broadest topic coverage (Figure 6).

Historically, there has been a clear bias toward species distribution, population size and human-carnivore interaction studies, whereas more recently evolved fields of research inquiry and topics requiring sophisticated analytical methods such as genetics, physiology, reproduction, and guild

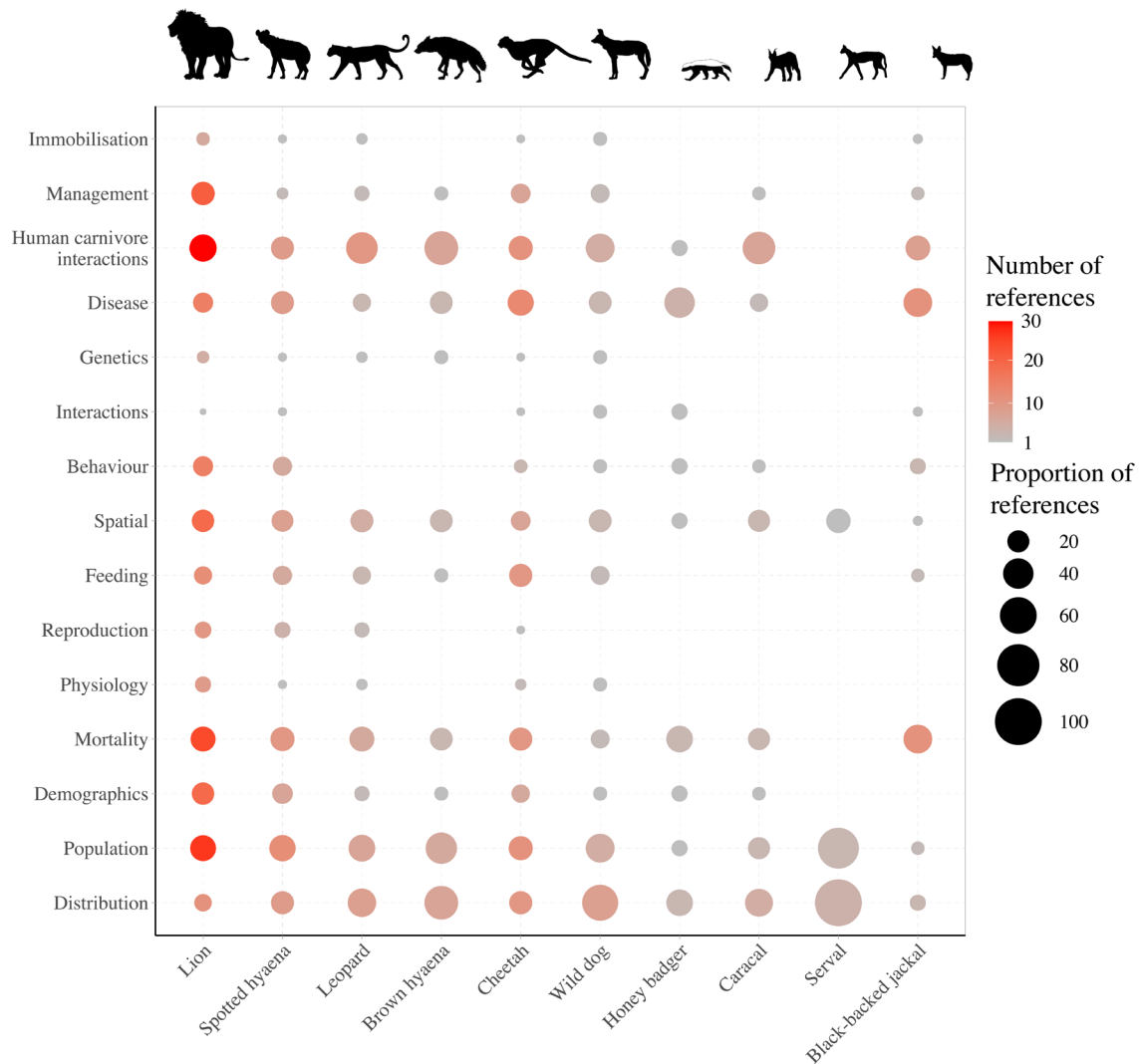


Figure 6: Matrix showing the relative distribution of specific study topics across all species and their relative contribution to all references for each species. Node size reflects the relative proportion each topic contributes to all references for each species whilst colour intensity signifies the number of references available for each species-topic node. Topic categories were not mutually exclusive; each reference could qualify for multiple categories. Thus, the sum of relative proportions may exceed 100%.

interactions have received much less attention (Figure 6). Except for lion and spotted hyaena, very little is known about the detailed demographics of carnivores in this landscape, and their behaviours (Figure 6). Carnivore occurrence, abundance (also local density) and movements were the only topics studied across all ten focal species, followed by mortality investigations, conflict surveys, and disease topics (Figure 6). The most frequently studied diseases were anthrax, feline immunodeficiency virus, and rabies (Appendix 2). Conflict studies often were descriptive, including investigations into livestock predation incidence, human perceptions of carnivores and evaluation of specific conflict management approaches such as the efficacy of translocations (Appendix 2). Human-carnivore interaction topics ($n = 25$) almost exclusively focussed on the damage caused by carnivores outside ENP (92%), particularly lion, with very little attention given to the values or benefits derived from carnivores in this landscape (16%). Methods studies were dominated by the development of chemical immobilisation procedures and contraception (Appendix 2).

DISCUSSION

The creation of an annotated digital bibliography of 139 key references applicable to carnivore research in the greater Etosha landscape has provided a good foundation to enable users to conduct literature searches, identify research gaps and prioritise future research directions. All key references, including those formerly in paper format, have been digitised and are available in a standardised format. This adds value in facilitating and improving accessibility, dissemination and safe keeping of records in a centralised repository at the EEI. We are confident that the synthesis and analyses of available materials were rigorous enough to the extent that the observed patterns and interpretation thereof yield an accurate reflection of the long-term trends in carnivore research.

The establishment of a permanent research section in 1965, which consisted of a veterinarian and two biologists, followed by the formal opening of the EEI in 1974 (Berry 1997) contributed greatly to stimulating carnivore research in ENP. Multiple factors, including an emphasis on focal species research by individual government-employed researchers dedicated to carnivore research were responsible for the observed increase in research output during the 1960s and 1980s (Figure 3a). Importantly, during the latter period, government-employed researchers were actively encouraged to register for postgraduate degrees at Tertiary Institutions, which promoted collaborative research projects and increased output of peer-reviewed publications. Notably, the majority of peer-reviewed

publications on carnivores could be attributed to only two government deployed researchers. The 1990s heralded a period of significant transition when Namibia gained its independence. Subsequently, staff re-structures, accelerated turnovers in staff, coupled with a diversification of research priorities were contributing factors to the observed decline in peer-reviewed publications by government-employed researchers specifically (Figure 3b). The decline in output, with a noticeable lag, was also evident amongst external researchers. Irrespective of author affiliation, the temporal decline in research output is continuing.

In general, the decline in research output over time, combined with a paucity of studies in communities surrounding ENP, calls for a need to initiate and expand research activities to communal and private lands. Taking cognisance of the larger human multiple-use system, such studies would cement the role of ENP, both as source of, and a safeguard for, carnivore populations, whilst also determining its importance in providing functional connectivity with other carnivore habitats in the geographic region. Etosha, as a National Park and important carnivore refuge, hosts a large diversity and abundance of carnivores. Therefore, the main functions and priorities of government-employed researchers were aligned to support research and monitoring programmes within the boundaries of ENP. This is evident from the study distribution pattern we found (Figure 4), which clearly illustrates a bias towards work within ENP boundaries as opposed to private and communal lands where most studies were restricted to conflict assessments.

The long-term trends and patterns across themes, species, and study topics (Figures 5 and 6) indeed correspond with global carnivore research patterns (Brooke *et al.* 2014). In southern Africa, ENP is the most important formal conservation area for carnivores in a semi-arid ecosystem. Although challenging, opportunities do exist and should be actively pursued to improve the functional connectivity of the greater Etosha landscape with other conservation areas located to the West and to the North-West into Angola, such as Iona NP. If this can be realised, the resultant joint management of resources across the existing boundary of ENP, would have a beneficial impact on carnivore conservation. The strong historic focus on a few charismatic large-bodied species, with particular emphasis on lion, likely reflects their public appeal and their immediate relevance for park management in terms of tourism value, impact on other species and, not least, conflict implications (Figure 5). Large species are also easier studied than cryptic smaller ones and usually attract more funding for research.

Our results provided a valuable platform to identify and highlight selected gaps in our current knowledge of carnivores in the greater Etosha landscape. Our main purpose in elucidating these is to provide the stimulus to promote and sustain long-term research across this area. Future research foci may, for instance, include:

- a) Identifying and quantifying both the ultimate and proximate drivers of carnivore fitness in this landscape, in terms of distribution and abundance, to ensure long-term species persistence.
- b) Although 27 disease studies have already been published, some of which ranged among the longest carnivore studies ever conducted in ENP, and more are currently underway, their emphasis was mostly on the prevalence and clinical manifestation of three diseases: rabies, anthrax, and feline immunodeficiency virus. Given an intensifying interface between wildlife, people, and domestic animals world-wide, disease studies may expand to include the role of carnivores and their parasites as disease reservoirs and vectors. Such studies would also help with disentangling the complex effects of changing habitats and climate on disease incidence and prevalence.
- c) To date, carnivore studies in the greater Etosha landscape have largely been of descriptive nature, and with a general focus on ecology and natural history, especially occurrence, abundance, diet, and movements patterns. Considering the complex challenges that protected areas and carnivores face (Ministry of Environment and Tourism 2015, Di Minin *et al.* 2016), it is expected that mechanistic and predictive studies will play a more prominent role in future, along with the increasing application of sophisticated methods such as conservation genetics.
- d) Currently, very little is known about carnivore physiology, behaviour, and communication, for instance, and how these might influence, or be influenced by, intra-guild processes. An increasing appreciation of the trophic complexity of carnivore landscapes (Montgomery *et al.* 2019) further suggests that future research should focus more on animal-environment interactions as well as trophic dynamics. Accordingly, greater importance should be placed on studying intra-specific and intra-guild interactions including both apex and meso-predators.
- e) A progression from simply documenting and describing carnivore impacts on land users around ENP to strategic, experimental testing of human-livestock-carnivore coexistence strategies (van Eeden *et al.* 2018) that acknowledge the dynamics and complexity of conflict. This also reflects the need to incorporate detailed information on livestock, stimulating a more holistic approach to conflict investigations (Weise *et al.* 2019).

- f) Considering the economic importance of carnivores for eco-tourism in southern Africa (Maciejewski & Kerley 2014, Van Der Meer *et al.* 2016), current research should be expanded to include positive and negative influences of tourism and other forms of commercial land use on carnivores and their management. Such studies should extend beyond ENP boundaries to represent the variety of stakeholders that benefit or accrue costs from carnivores, such as human settlements with livestock holdings, private tourism reserves and communal conservancies, or livestock and game ranches. Similarly, anthropogenic influences on carnivores and their habitat associated with tourism, such as the development of artificial waterholes and fencing deserve greater research attention.

However, none of the above-mentioned suggestions should occur at the expense of detailed biological investigations and natural history research, as these form the foundation of our understanding of how carnivores utilise their environment and adapt to special circumstances. We also regard the importance of long-term research as a crucial prerequisite for addressing these knowledge gaps. Long-term ecological studies contribute to an understanding of how species and ecosystems respond to a spatially and temporally changing environment. Studies conducted over prolonged time periods can reveal important patterns and provide insights into ecological processes that would otherwise go unnoticed (Hughes 2013, Taig-Johnston *et al.* 2017, Melzheimer *et al.* 2018). In reference to the long-term anthrax research programme in ENP, Carlson *et al.* (2018), illustrated the importance of an interdisciplinary approach where key advances have been made in exemplifying the complexities of the enzootic process. Lindenmayer *et al.* (2012) identified five key values of long-term ecological studies, which are:

- “(1) quantifying ecological responses to drivers of ecosystem change;
- (2) understanding complex ecosystem processes that occur over prolonged periods;
- (3) providing core ecological data that may be used to develop theoretical ecological models and to parameterise and validate simulation models;
- (4) acting as platforms for collaborative studies, thus promoting multidisciplinary research; and
- (5) providing data and understanding at scales relevant to management, and hence critically supporting evidence-based policy, decision making and the management of ecosystems”.

In recognition of the value of an interdisciplinary approach (Carlson *et al.* 2018) as well as applying the key values identified by Lindenmayer *et al.* (2012), we believe that a long-term carnivore research programme in the greater Etosha landscape should be

implemented and encouraged. The management of such an initiative, where data are gathered on a variety of topics by different institutions over decades, is challenging. Both private and government institutions thus play a crucial role in leading and coordinating research effort, in fostering collaborations, in archiving the data collected, in synchronising efforts across time and organisations, and in providing directions for future research. Given the global importance of Etosha as a carnivore stronghold, Namibia, through the EEI, is ideally placed to stimulate, facilitate, and strengthen long-term carnivore studies in collaboration with local and international partners.

The scope and focus of this synthesis should further be expanded by consolidating information from literature sources with the great number of raw data accounts, many of which have yet to be analysed and published, that different organisations have gathered for future in-depth meta-analyses. Detailed topic- and species-specific reviews of the existing contents and results would provide additional important insight into the current state of knowledge.

In conclusion, we encourage similar stocktaking and synthesis exercises for other biological taxa and research topics with a long research history in ENP, as well as for other similarly important carnivore strongholds with historical data such as the Serengeti NP in Tanzania, or Kruger NP in South Africa. Specifically, with regards ENP, the EEI archives hold a tremendous amount of environmental information that extends far beyond the field of carnivore research, some of which has yet to be analysed comprehensively. Preserving this existing knowledge and merging it with information gathered by other organisations is a priority. No less important is to ensure that the information is readily available, which provides prospective studies with a comprehensive overview of historical work conducted. It also enables a rare and valuable perspective on how changes have occurred in this landscape for carnivores, and the ecosystem with all its components. Ultimately, this could drive the identification and prioritisation of future studies.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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