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Present distribution of common hippopotamus populations in southern Africa, and the need for a centralised database

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ABSTRACT

The geographical range of common hippopotamus' (*Hippopotamus amphibius*) has retracted over the last century as a result of anthropogenic pressures. At present, extant common hippopotamus (hereafter, hippo) populations are fragmented and largely constrained to Protected Areas. There is an urgent need for conservation management, but data and information on the spatial ecology of hippos to base conservation strategies on are lacking. Without a centralised and collaborative database that documents their distribution and abundance, comprehensive population assessments remain a challenge. This study establishes a detailed spatial database of hippo population estimates and distribution across southern Africa, by collating recent survey data from a range of sources, facilitating population monitoring and informed conservation decision making. Drawing from a review of the primary literature, grey literature, aerial surveys, websites, and expert input, we provide a comprehensive geographic range map for hippos and evaluate hippo distribution within Protected Areas. Our review reveals several discrepancies between our data and previous hippo distribution and abundance estimates. We also highlight inconsistent methods used to survey hippo populations across southern Africa. By identifying twelve regions with large populations of hippos (>1000 individuals), our findings underscore the importance of extensive and well-connected Transfrontier Conservation Areas to support large, dense hippo populations. We encourage the IUCN SSC Hippo Specialist Group to promote standardised and coordinated surveys and progress a spatial database of hippo distribution and abundance across the rest of Africa.

1. Introduction

Over the last century, megaherbivores have experienced substantial range contractions and population declines due to rising human-induced pressures such as land-use changes, unsustainable hunting, and livestock competition (Ripple et al., 2015). Megaherbivores are large-bodied species of herbivorous mammals that attain adult body mass in excess of 1000 kg (Owen-Smith, 1988). Globally, there are nine extant terrestrial megaherbivore species, with six of these occurring in Africa (Owen-Smith, 1988). Megaherbivores are ecologically important, as they play vital roles as ecosystem engineers through exerting top-down control over vegetation composition and structure (Malhi et al., 2016; Ripple et al., 2015). Furthermore, megaherbivores contribute to socioeconomic development through tourism revenue and their high cultural value (Lindsey et al., 2007; van Houdt and Traill, 2022). Losses of remnant populations reduce the functional resilience of ecosystems due to reduced nutrient cycling rates and changes in geomorphological processes (Gill, 2014).

At present, the persistence of extant megaherbivores relies heavily on conservation efforts (Hoffmann et al., 2015), as evidenced by past successes in re-establishing declining species such as the greater one-horned rhinoceros (*Rhinoceros unicornis*) in South Asia (Rookmaaker et al., 2016). Nevertheless, megaherbivore conservation research in Africa over the last 50 years has been taxonomically biased towards the African savanna elephant (*Loxodonta africana*) and geographically biased towards internationally recognised Protected Areas with a high capacity for wildlife monitoring (Hyvarinen et al., 2021). Declining populations, range retractions, and fragmentations of African megaherbivore species (Ripple et al., 2015), such as white rhinoceros' (*Ceratotherium simum*), giraffes (*Giraffa camelopardalis*), and common hippopotamus' (*Hippopotamus amphibius*) have therefore triggered the need to attain a baseline understanding of their distribution and

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numbers across broad scales.

Common hippopotami (hereafter, hippos) play a pivotal role as ecosystem engineers in both terrestrial and freshwater realms (Field, 1970; Subalusky et al., 2015) and have recently been described as the most ecologically influential African megaherbivore (Voysey et al., 2023). As vectors of resource subsidies from savanna grasslands into aquatic systems, hippos facilitate biogeochemical cycling through the transfer of vital nutrients such as nitrogen and phosphorus, as well as organic matter, carbon, and silica, which supports both primary and secondary aquatic productivity (Schoelynck et al., 2019; Subalusky et al., 2015; Voysey et al., 2023). Hippo trails, formed through trampling and wallowing, also significantly alter the geomorphology of freshwater systems by carving gullies, creating new river channels, and widening riverbanks (McCarthy et al., 1998; Voysey et al., 2023). Notably, their specialised ecological roles cannot be replicated by another species of extant megaherbivore (Voysey et al., 2023).

Hippos may be important to freshwater systems, but they are also reliant on those systems. They require access to rivers, wetlands, and lakes with a preferred depth of approximately 0.5–1.49 m for diurnal refuge (Prinsloo et al., 2020). They also require access to grazing areas for nocturnal foraging, and these are typically situated within 10 km from water sources (Onyeanusi, 2004; Owen-Smith, 1988; Prinsloo et al., 2020). Historically, hippo populations were once ubiquitous across Africa, occurring wherever suitable water bodies existed (Owen-Smith, 1988). Increasing anthropogenic pressures on African landscapes over the last century have, however, reduced the available area of occupancy for hippos, resulting in substantial population declines (Eksteen et al., 2016; Kanga et al., 2011; Lewison, 2007).

Range-wide, hippo populations are declining by approximately 6–8 % per annum (Utete, 2020). Hippos are particularly threatened by losses of suitable terrestrial and freshwater habitats, human-wildlife conflicts including illegal poaching for meat and ivory, and climate change (Eksteen et al., 2016; Kanga et al., 2011; Snyder, 2015). As a result, remnant hippo populations are generally constrained to Protected Areas (PAs) (Chakuya et al., 2024; Fritsch et al., 2021; Lewison and Pluháček, 2017; Stoffel et al., 2015).

Hippos are classified as ‘vulnerable’ by The International Union for the Conservation of Nature (IUCN) Red List (Lewison and Pluháček, 2017). The latest species assessment in 2016 estimated 115,000–130,000 individuals across Africa (Lewison and Pluháček, 2017). According to the IUCN, the southern African region currently represents one of the last remaining conservation strongholds for the species (Lewison and Pluháček, 2017). Yet, hippo population estimates for some countries in previous Red List assessments are inaccurate due to the use of outdated information (Mackie et al., 2013; Roth et al., 2004). A recent CITES (2022a) analysis updated the population assessments for hippos in selected countries across Africa, and found substantial population underestimates in the 2016 IUCN Red List assessment for Tanzania, Botswana, Mozambique, and South Africa. In Botswana, for example, the CITES hippo population estimate of >20,000 individuals based on recent surveys considerably exceeds the IUCN estimate of 2000–4000 individuals. This example supports a lack of coherent data on hippo abundance and distribution across the sub-region.

Despite their ecological importance, the spatial ecology and the impacts of human-related threats on hippos are not well understood, compared to other megaherbivores, such as savanna elephants (Stears et al., 2019; van Houdt and Traill, 2022). Hippos' limited scientific attention may stem from challenges in studying them in the field, such as their nocturnal habits, their aggressive behaviour, and a tendency to submerge in response to noise (Inman et al., 2019). The lack of an established system for monitoring hippo populations further complicates the availability of accurate and comparable population estimates. Since survey methods for hippos are not standardised, various techniques are employed, such as aerial (fixed-wing, helicopter, drone), boat, and ground surveys, with varying standards, sampling approaches, and at different times of year (Inman et al., 2019; Kujirakwinja, 2010; Utete, 2020). While GPS radio tracking devices are widely used to reveal insights into the spatial ecology of other megaherbivores (e.g. Deacon and Smit, 2017; le Roex et al., 2019; Wall et al., 2024), it is complicated to immobilise hippos and find suitable attachment devices that can withstand their semi-aquatic lifestyle (Voysey et al., 2023; Stears et al., 2019).

Many wildlife surveys overlook hippos entirely (Linchant et al., 2018; Lindsey et al., 2014), and if they are included, it is typically as part of broader large mammal counts. While age- and sex-specific vital rates have been recorded for hippos (Laws, 1968; Smuts and Whyte, 1981), collecting detailed demographic data in the field poses challenges. Hippos exhibit minimal sexual dimorphism (Shannon et al., 2021) and tend to remain submerged under water for long periods, complicating efforts to estimate body size for ageing (Inman and Leggett, 2022). As a result, the accuracy of hippo count and demographic data is generally low, especially for large aggregated groups (Linchant et al., 2018). Consequently, broad-scale hippo population assessments remain challenging, making it difficult to monitor population estimates and trends, and to implement effective conservation actions.

Monitoring long-term population trends permits the reliable classification of the conservation status of a species, in turn allowing for the development of clearly defined and objective management decisions (Moreno et al., 2023; Robinson et al., 2018; White, 2019). The provision of accessible databases of organised and comprehensive information on species occurrence is essential to verify these trends and effectively conserve populations (Blanc et al., 2007). In recent decades, spatial databases that estimate population sizes and distributions have been developed for most of Africa's megaherbivores. Examples of these databases include those for elephants (Said et al., 1995), rhinos (Knight, 2024), and giraffes (Brown et al., 2021). Hippos currently remain the only terrestrial African megaherbivore without a centralised spatial data repository in development.

Here, we addressed this disparity and assess and document known occurrences of hippos across southern Africa from 2003 to 2023. Our key objectives were to 1) determine the current distribution of hippos within and beyond Protected Areas, 2) create an updated geographic range map for hippos across southern Africa, and 3) compare our findings with the best available information on hippo distribution and the most recent country-wide population estimates, including those available through the IUCN Red List assessments.

2. Materials and methods

We compiled a database containing information on hippo occurrence in nine countries across southern Africa: Angola, Botswana, Eswatini, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe, defined in accordance with Said et al. (1995).

We targeted southern Africa initially because of access to local expertise, and the common use of English in the region. Our work is however a first step towards an Africa-wide spatial database of common hippo population estimates and distribution.

Our data collection approach followed the framework of a systematic review (Page et al., 2021), with adaptations to incorporate supplementary data sources. This process comprised: 1) conducting a comprehensive review of the primary literature, 2) executing targeted web searches in grey literature and on websites, 3) evaluating aerial-survey data, and 4) collating information provided by subject-matter experts. We determined records of hippo presence in PAs, riverine systems, lakes, and dams, and collated population estimates where they were available. Presence records were defined as ‘the recent documentation of hippo occurrence within a specified geographic area’. In PAs, we supplemented our database with absence records derived from government websites and grey literature. Here, we define absence records as ‘recently confirmed absence of hippo within a specified geographic area’, and notably this differs to ‘unknown’. Here, ‘unknown’ was defined as ‘a lack of confirmed presence or absence of hippos in a defined geographic area'. We note that absence records were typically available for PAs, given that these were the areas where surveys were reliably conducted. To assess the recent history of population trends, our assessment spanned the past two decades, encompassing the years 2003–2023, which constitutes two hippo generations (Pacifici et al., 2013). However, we included primary literature from 1960 to 2023 to aid in the development of an additional database of historical records.

2.1. Primary literature review

Electronic searches were done through the Web of Science Core Collection (https://www.webofscience.com), Scopus (https://www.scopus.com), and Google Scholar (https://scholar.google.com) databases. We searched the title, abstract, and keywords using the strings: "common hippopotamus" OR "common hippo" OR "*Hippopotamus amphibius*" OR "*H. amphibius*" OR "*H amphibius*". The criteria for data inclusion were 1) correct taxonomic identification as *H. amphibius*, 2) description of a location within southern Africa, and 3) year of data collection (Supporting Information for details of search strings). We chose the date range of 2003–2023 as it coincides with improved documentation of hippo occurrence throughout the sub-region, thereby facilitating accessible data. We also included additional literature recommended by subject-matter experts. The protocol and management of the literature review was performed through CADIMA (Kohl et al., 2018), an open access, web-based systematic review support tool. The review process ensured compliance to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (see Page et al., 2021).

2.2. Grey literature and websites

We conducted targeted web searches to explore grey literature within the Google Scholar database, Convention on International Trade in Endangered Species of Wild Fauna and Flora documents (CITES, https://cites.org/eng/meetings/cop), Environmental Information Service Namibia database (http://the-eis.com/elibrary/), Ramsar Sites Information Service database (https://rsis.ramsar.org), and on websites for non-governmental conservation organisations that were involved in managing one or more PAs in the region. We further scanned national government department websites for each country for information on hippo presence or absence. We excluded media articles, or any websites that were not affiliated with either government or non-government conservation organisations (Supporting Information).

2.3. Aerial survey data

We compiled aerial observation data for hippos across northern Botswana from 2001 to 2022, derived from a series of surveys conducted by the Non-Government Organisation Elephants Without Borders (https://elephantswithoutborders.org) and the Department of Wildlife and National Parks (Botswana). These surveys primarily targeted elephants, but also recorded other wildlife species, including hippos. Our database features counts from the latest survey in 2018, which covered an area of 103,662 km^2 using a small fixed-wing plane (see Chase et al. (2018)). In addition, we drew upon part-published and unpublished aerial survey records for hippo occurrences in Kruger National Park (South Africa) from 1984 to 2022, sourced through South African National Parks. We also incorporated data from multiple private nature reserves within the Associated Private Nature Reserve (APNR) system, supported by field personnel and the Agricultural Research Council (South Africa). Furthermore, we integrated aerial survey data from Gorongosa National Park (Mozambique) spanning 1997–2022. Various published aerial survey records from grey literature sources were also utilised (African Parks, 2020; Beilfuss et al., 2010; Bussière and Potgieter, 2023; Chase, 2009; Chase et al., 2018; CITES, 2017; Craig, 2012; Craig and Gibson, 2019; Dunham, 2004; Dunham, 2010; Dunham et al., 2015; Hanekom and Cumbane, 2016; Kuvawoga and Gandiwa, 2011; WCS Flight Programme, 2009; Reece et al., 2021; Shanungu et al., 2015).

2.4. Expert knowledge

We obtained unpublished records by using the most recent 2016 IUCN spatial range map (https://www.iucnredlist.org/resources/spatial-data-download) and citizen science records derived from the Global Biodiversity Information Facility (https://www.gbif.org) as guides. We overlayed these spatial layers with a map of PAs from the World Database on Protected Areas (WDPA, https://www.protectedplanet.net), and conducted web searches to obtain contact details for reserve managers/wardens where one or both layers indicated hippo occurrence. Further searches for relevant personnel were targeted to governmental organisations and researchers working in the field of African megaherbivore conservation (Supporting Information for a full list of targeted organisations and PAs). To reduce geographical bias towards PAs, we asked all contacted personnel for information on the occurrence of hippos in surrounding unprotected lands as well. All communications were conducted between March – November 2023 by email to request records of hippo occurrence, and to suggest other potential contacts. Where experts chose not to communicate, we recorded those PAs as having unknown hippo occurrence.

2.5. Survey methodology

We extracted information on the methods used to derive population estimates for presence records in our database, where available. We provide a summary of common survey methods employed to count hippos (Supporting Information). To analyse the frequency of methods applied in our data, we determined the total number of populations surveyed and the total number of individuals counted using each method.

2.6. Large populations and range discrepancies

We identified regions that represent large populations for hippos across southern Africa. We defined large populations of hippos to consist of >1000 individuals (since 2003), similar to thresholds used for elephants (Huang et al., 2024; Naidoo et al., 2016).

We also compared the total abundance records obtained for each country with the most recent reliable population estimate by either the IUCN (Lewison and Pluháček, 2017), CITES (2017, 2022a), or the South African National Biodiversity Institute (Eksteen et al., 2016). We identified discrepancies between the number of regions found with hippo presence compared with the latest assessment by the IUCN (Supporting Information). We defined regions using political provinces or districts within each country. We obtained data and/or information from the literature or from expert knowledge for all nine assessed countries (Supporting Information).

2.7. Mapping range and protected areas

We used ArcGIS Pro (Version 3.1.0) to derive maps. We generated range maps using shapefiles of PAs, rivers, lakes, and dams. We included PAs based on their inclusion in the WDPA (UNEP-WCMC and IUCN., 2024). Rivers, lakes, and dams were incorporated in the mapping process if they are included in the HydroATLAS database (Lehner et al., 2022; Linke et al., 2019).

To further assess the distribution of hippos within PAs, we overlaid our hippo range map onto a map of all PAs from the WDPA. We mapped both presence and absence records within PAs to highlight where information remains unknown across the region. If hippo occurrence within a Protected Area was only recognised by the 2016 IUCN range map, with no further data to substantiate it, we defined occurrence in that area as unknown. Where hippos were present, we extracted data on the governance type from the WDPA to assess the distribution of country-wide presence within government-managed protected areas (GMPAs) and alternative-managed protected areas. We defined GMPAs as PAs with a governance type of 'governance by government' or 'shared governance' following O'Connor et al. (2019).

3. Results

Our database consists of 199 records of hippo presence, representing 62 regions (distinct provinces/districts) across nine countries. We sourced unique data from 20 scientific papers, 28 grey literature documents, 38 webpages from government department and non-governmental conservation organisation websites, and 18 subject-matter experts. Our literature review resulted in 89 papers with records of hippo occurrence in southern Africa from 1960 to 2023 (Supporting Information).

We identified twelve regions across southern Africa that contain large populations (>1000) of hippos (Fig. 1). These regions spread across southern Africa and cover seven of the nine countries assessed (with no large populations in Angola and Eswatini). According to our data, the Luangwa River (Zambia) and surrounding PAs currently support the largest hippo population in southern Africa (Table 1). All regions containing large hippo populations are within current Transfrontier Conservation Areas, except for the Shire River (Malawi).

Hippos are present and absent in PAs across southern Africa (Fig. 2). We obtained 178 records of presence in PAs across all nine assessed countries, and 135 records of absence for seven countries (with no absence records for Eswatini or Malawi). Widespread data gaps remain, as demonstrated by the scale of unknown information on either presence or absence of hippos in PAs.

We produced an updated geographic range map for hippos over a 20-year period between 2003 and 2023 (Fig. 3), based on our derived database (Supporting Information). Hippo distribution appears to be largely restricted to PAs, with some presence along major river systems that span both protected and unprotected lands.

The proportional representation of the governance type in PAs with hippo presence varies by country (Supporting information). In Mozambique, Botswana, and Malawi, over half of the PAs that host hippo populations are GMPAs. Conversely, in Namibia, over 75 % are governed by communities and/or private landowners. In South Africa, there is an almost equal distribution of hippos within GMPAs and alternative-managed protected areas. Governance type for PAs in Angola and Zimbabwe is currently not reported by the WDPA and therefore could not be assessed (UNEP-WCMC and IUCN., 2024).

The hippo population estimates in our database were derived from seven survey methods: aerial (fixed wing, helicopter, and unknown), boat, ground, informed guess, and photographic. Aerial surveys, which accounted for the majority of counts where the survey method was provided, were the most frequently used, covering 93 populations and 73 % of documented surveys (Table 3). Ground surveys, used for 3

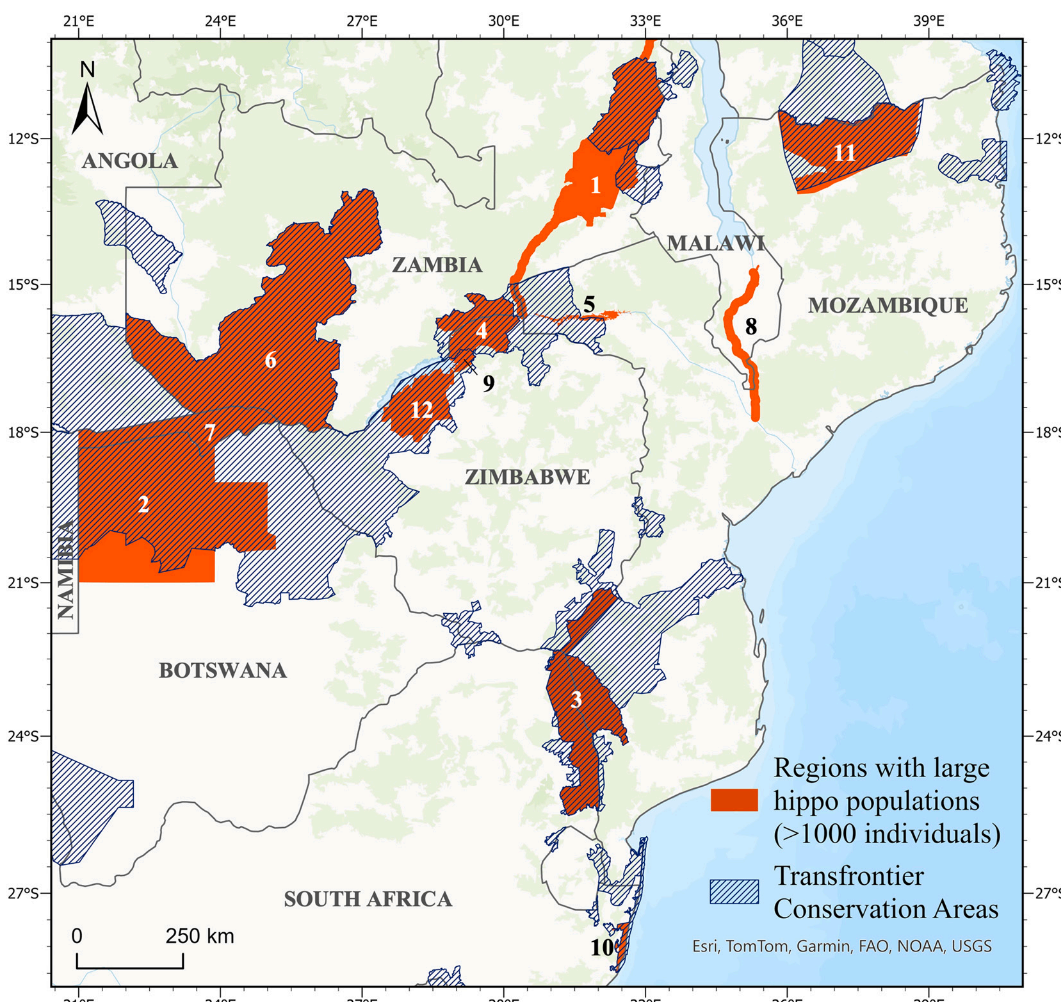

Fig. 1. Spatial distribution of large populations of hippos (>1000 individuals) across southern Africa (as orange polygons). Also shown are present day Transfrontier Conservation Areas (TFCA). The TFCA names matching the numbers above are provided in Table 1, as well as animal abundance estimates. Hippo populations do not occur across the full extent of the regions indicated.

Table 1
Summary of population estimates where large populations (>1000 individuals) of hippo occur in southern Africa.[a]

Large populations of common hippos across southern Africa (>1000 individuals)	Pop. estimate
1. Luangwa River, Zambia	~25,000
2. Ngamiland District (incl. Okavango Delta World Heritage Site), Botswana	>12,500
3. Great Limpopo Transfrontier Conservation Area (incl. Kruger National Park (South Africa), Limpopo National Park (Mozambique) & Gonarezhou National Park (Zimbabwe))	>5700
4. Lower Zambezi - Mana Pools Transfrontier Conservation Area, Zambia & Zimbabwe	~5000
5. Lake Cahora Bassa, Mozambique	>4000
6. Kavango-Zambezi Transfrontier Conservation Area (Kafue Region), Zambia	>3500
7. Kavango-Zambezi Transfrontier Conservation Area (Kavango Zambezi Region), Namibia	~3000
8. Shire River (incl. Liwonde National Park, Majete Wildlife Reserve & Elephant Marsh Ramsar Site), Malawi	>2600
9. Matusadona National Park, Zimbabwe	~2100
10. St Lucia System, KwaZulu-Natal, South Africa	>1200
11. Niassa District, (incl. Niassa Special Reserve & Rovuma River), Mozambique	>1100
12. Kavango-Zambezi Transfrontier Conservation Area (Sebungwe Region), Zimbabwe	>1000

[a] Also provided are the names of each Protected Area, including Transfrontier Conservation Areas. The numbers here correspond to Fig. 1.

populations, recorded over 25,200 hippos, with notable usage along the Luangwa River in Zambia. Boat surveys covered 11 populations, representing 9 % of surveys. Photographic methods were used infrequently, while seven surveyed hippo population estimates (representing 5 % of surveys) were derived by informed guesses. Notably, thirteen populations had unknown survey methods, and 71 surveys had no available data, and therefore survey methods could not be evaluated.

From our data, we estimated ~87,000 common hippos throughout the region between 2003 and 2023. These values are greater than the 2016 population estimate by the IUCN Red List assessment (of 60,000 hippos across southern Africa), although of course, these are crude population estimates. Furthermore, in comparison to the latest reliable population estimates from other sources, our findings reveal some discrepancy on a country-wide scale (Table 2).

We observed additional locations occupied by hippos in four countries compared with the latest IUCN range map (Supporting information). Notably, Gorongosa National Park (Mozambique), Sioma Ngwezi National Park (Zambia), and Luengue-Luiana National Park (Angola) are missing from the IUCN range map.

We also note some areas listed by the IUCN as having hippo present, but where the species no longer occurs. In Angola, there are no longer hippos in PAs in the Cunene and Huila Plateau (indicated by the IUCN as having hippos present). Similarly, for the West Kunene region in Namibia, we found no evidence of hippo presence. This finding was corroborated by expert opinion in the region (J. Paterson, pers. comm).

Moreover, we could not find hippo records to correspond with the 2016 IUCN range map for two regions, one in Angola and the other in Malawi (Supporting information).

4. Discussion

Common hippopotamus populations are distributed across southern Africa, although the species no longer occurs across most perennial river systems, as they once did (Owen-Smith, 1988). Notably, we found that hippos now predominantly occur within PAs, and large populations are supported by Transfrontier Conservation Areas (TFCAs). We also found some notable omissions in the best available data available through the IUCN Red List, confirming the need for an up-to-date, Africa wide spatial database for hippos, as has been done for elephants (Said et al., 1995). We have gone some way towards achieving this, by providing a comprehensive database of hippo population estimates and distribution for southern Africa (Supporting Information).

While the role of TFCAs in megaherbivore conservation has been previously documented for elephants (Naidoo et al., 2024; Lindsay et al., 2017; Roque et al., 2022), their impact on hippos has not been explored. Our findings suggest that extensive, transboundary TFCAs support large hippo populations by protecting vast, inherently connected water systems. The reduced need for large seasonal aggregations in freshwater habitats consequently lowers disease risk and intraspecific competition for resources, ultimately limiting mortality (Owen-Smith, 1988). Additionally, coordinated conservation strategies between neighbouring countries improve law enforcement capacity and the regulation of national laws pertaining to water management, enhancing resource availability (Mason et al., 2020; Dunham et al., 2010). Increased protection also reduces the potential for anthropogenic threats such as agricultural cropping and water abstractions for irrigation, which may reduce water quality and diminish surface water availability, respectively. Thus, improved connectivity between PAs facilitated by TFCAs (Mpofu et al., 2023), is critical for sustaining large regional hippo populations, underscoring the importance of continued efforts to promote and expand these international agreements.

The absence of a centralised repository of spatial data, as per the African Elephant Database (AED), has impeded targeted conservation efforts and hindered our ability to comprehensively assess and address the drivers of hippo decline. In the latest IUCN assessment, for example, concern was expressed for the conservation status of hippos in over half of the countries in southern Africa with overall recommendations for research into population sizes, distribution, and trends, as well as threats and actions (Lewison and Pluháček, 2017). Given rising anthropogenic pressures and limited financial resources for hippo conservation (Prinsloo et al., 2020; van Houdt and Traill, 2022), targeted and objective management actions are imperative. Access to recent, robust spatial data for hippo distributions and abundances will facilitate spatially explicit conservation decision making, informing current conservation priorities and guiding effective management strategies (Stephenson and Stengel, 2020).

Existing databases for other megaherbivores offer significant conservation value. For example, the AED, established in 1986, has facilitated diverse conservation research for elephants, including population trend analysis (Blanc et al., 2005; Bouché et al., 2011; Chase et al., 2016; Lindsay et al., 2017), density modelling (De Boer et al., 2013; Robson et al., 2017), and conservation planning (Litoroh et al., 2012; Stephenson and Ntiamoa-Baidu, 2010; Zacarias and Loyola, 2018). In contrast, research of similar depth is lacking for hippos, despite the detrimental impacts of high hippo population densities on vegetation and aquatic processes (Stears et al., 2018), and the direct influence of anthropogenic pressures on their population persistence (Eksteen et al., 2016; Kanga et al., 2011; Stommel et al., 2016).

Severe declines or extirpations of hippos may lead to substantial changes in geomorphological and ecological processes (McCarthy et al., 1998; Voysey et al., 2023). For instance, losses of nutrient-rich hippo dung deposits into freshwater systems may significantly reduce aquatic productivity, diminishing the abundance and diversity of aquatic organisms (Subalusky et al., 2015; Voysey et al., 2023). Moreover, fewer

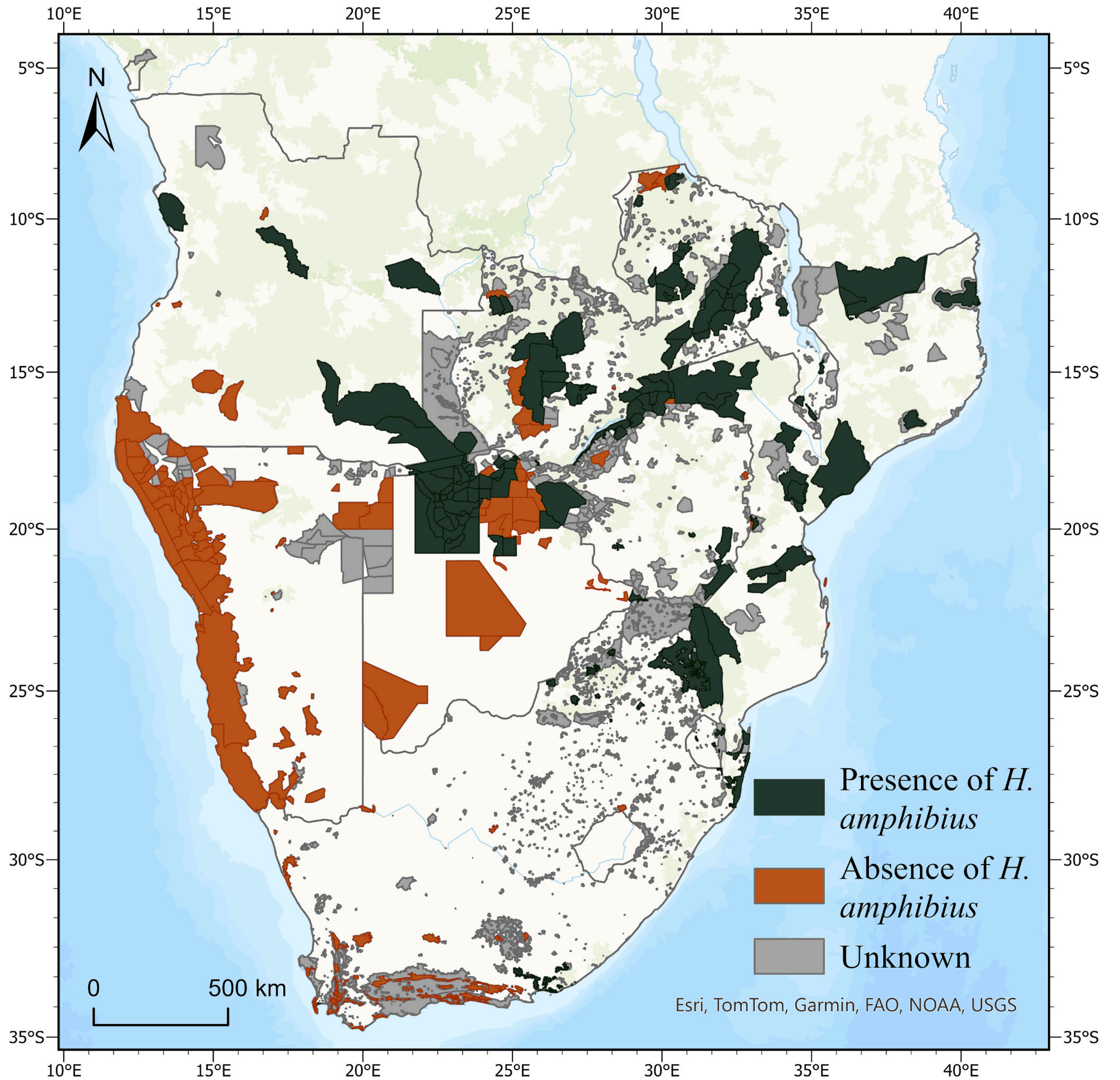

Fig. 2. Protected Areas across southern Africa, with data showing the known presence of hippo (dark green), confirmed absence (orange), or unknown occurrence (grey). Data here are derived from records dating 2003–2023. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Protected Area data from World Database on Protected Areas, https://www.protectedplanet.net.

grazing lawns will likely increase fire prevalence and alter habitat use for mesoherbivores (McCauley et al., 2018). Therefore, continued development and updates of a spatial database of hippo population estimates and distribution incorporating comprehensive data is crucial for projecting current and future population trends, thereby facilitating reliable classification of their conservation status.

The IUCN Red List is the most authoritative and reliable source of information on the conservation status of wild species. However, here we show that there may be some omission of data on the current distribution and abundance of hippo populations in southern Africa (Supporting Information). Given the anthropogenic impacts on hippo populations (Baker et al., 2022; Tefera et al., 2024), observed increases in range by region in our range map are likely due to the inclusion of a more comprehensive and detailed assessment rather than range expansion or population growth. This improved dataset, compared with the IUCN range map, provides a more accurate representation of hippo distribution by incorporating better survey data from existing sources. Many of these newly identified populations are small and isolated, occurring in small lakes and river sections, small reserves, and artificial water systems. Nonetheless, some previously unrecognised populations by the IUCN range map are larger, such as hippos in Gorongosa National Park, Mozambique (>500 individuals). On the other hand, hippos in Angola were subject to direct human persecution for the duration of the Angolan Civil War between 1975 and 2002 (Beja et al., 2019). Local extirpations in these areas, and thus the range contractions shown on our range map, are most likely the result of unregulated hunting for the

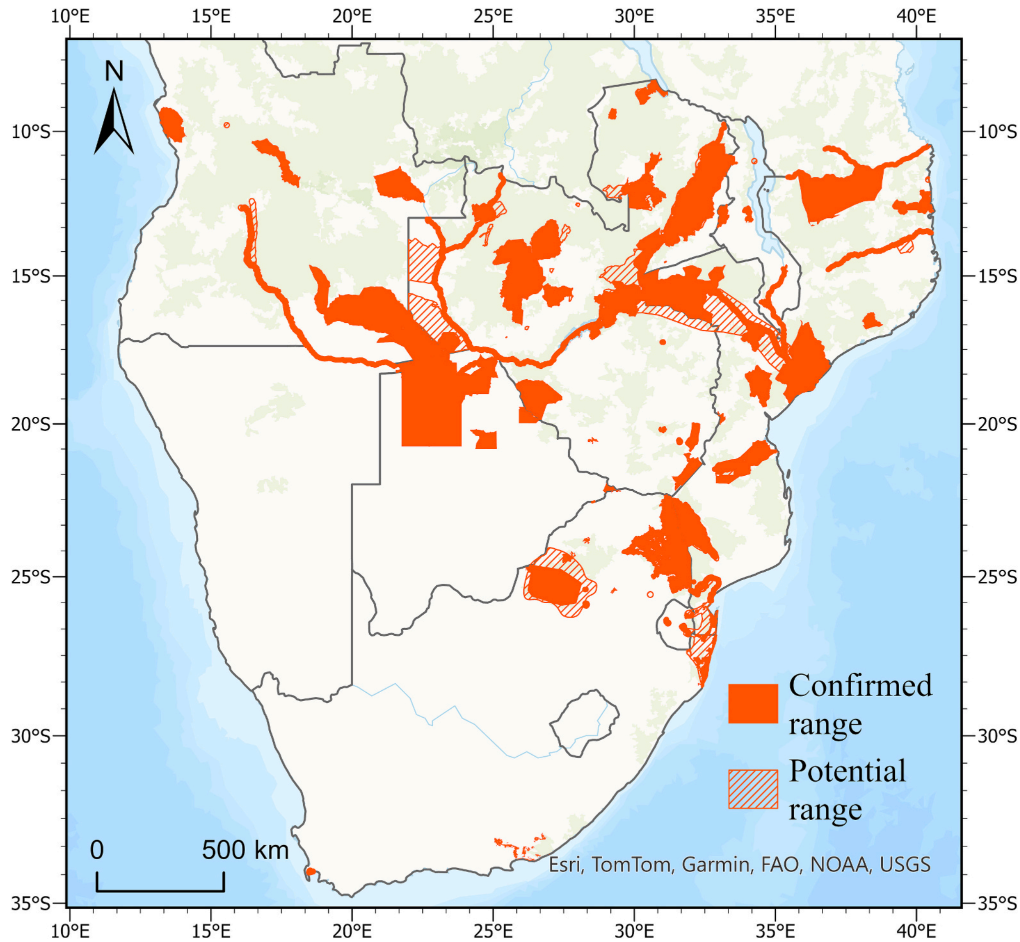

Fig. 3. Geographic range map for common hippopotamus in southern Africa, in 2023. Confirmed range in filled orange polygons. Hatched polygons represent unconfirmed ranges (indicated in the 2016 IUCN range map as 'hippo present' but cannot be confirmed from our study.

Table 2
Summary of recent published population estimates and trends for hippo for each country in southern Africa and the abundance estimates derived in this study.

Country	Most recent population estimate	Total abundance records found in this study (~n)	Most recent population trend
Angola	500[a]	>220	Decreasing[a]
Botswana	20,000[b]	>13,200	Decreasing[a]
Eswatini	150[a]	0	Stable[a]
Malawi	>3000[b]	>2800	Stable[a]
Mozambique	>8000[c]	>10,400	Stable[c]
Namibia	3300[a]	>3000	Increasing[a]
South Africa	11,061[d]	>9200	Stable[e]
Zambia	40,000–45,000[a]	>38,400	Stable[a]
Zimbabwe	>5000[b]	>9600	Stable[a]
Totals	**~91,011–96,011**	**>86,800**	**Overall trend: stable**[a]

[a] Lewison and Pluháček (2017).
[b] CITES (2022a).
[c] CITES (2017).
[d] Eksteen et al. (2016).
[e] CITES (2022b).

Table 3
Survey methods used to derive hippo abundance estimates across individuals (~n) and populations (n) in this study.

Survey method	Individuals counted (~n)	Populations surveyed (n)
Aerial (fixed-wing)	>29,700	59
Aerial (helicopter)	>16,600	30
Aerial (unknown)	>2500	4
Boat	>8600	11
Ground	>25,200	3
Informed guess	>110	7
Photographic survey	~2100	1
Unknown	>2050	13
Totals	**>86,800**	**128**

meat trade and human-wildlife conflict resolution over the last 50 years, as demonstrated in Quiçama National Park and Quiçama Game Reserve, Angola (Braga-Pereira et al., 2021).

Hippo populations are relatively small and fragmented in Angola, Eswatini, and Malawi. This geographic fragmentation may limit gene flow and eventually lead to genetic isolation (Beckwitt et al., 2016; Eksteen et al., 2016), as observed in other megaherbivores such as black rhinos (*Diceros bicornis*) in South Africa (le Roex et al., 2018). Small and isolated populations of hippos may be particularly vulnerable to disturbances due to their highly specific habitat requirements. Owing to these requirements, hippos may face extirpation in areas subject to high pressures, such as aquatic systems with high levels of water abstraction from human settlements in riparian zones, and they have been observed to extend their ranges by up to 15 km during drought conditions (Dunham et al., 2010; Kanga et al., 2011; Stears et al., 2019; Stommel et al., 2016). Populations inhabiting water systems that act as Protected Area boundaries or international borders may be forced into unprotected land in the search for resources, exposing them to further anthropogenic pressures and human conflict potential (Dunham et al., 2010; Kanga et al., 2011). As such, sustaining genetic diversity while increasing protection of land outside of formal PAs may be integral to their persistence, emphasising the importance of the development of transboundary migratory wildlife corridors. This approach underscores the urgency of coordinated conservation efforts to mitigate the effects of habitat fragmentation on hippo populations.

On a national scale, we found the Luangwa River (Zambia) and surrounding PAs to support the largest hippo population in southern Africa. The Luangwa network of unfenced PAs allows free movement of wildlife (Huang et al., 2022) while the expansive grasslands and presence of lagoons and meanders as a result of river course changes provide high quality habitat to support dense hippo populations (Chansa et al., 2011; Chomba et al., 2013). The relatively high numbers of hippo in the Luangwa River does imply that these populations are robust in the face of future change. Nevertheless, anthropogenic threats may increase along the Luangwa River (Irvine et al., 2019; Watson et al., 2015), with unknown extent of future habitat loss, or changed river flows under climate change that may drive these hippo populations into decline (Hamududu and Ngoma, 2020). Hippos are predated on by lions in the Luangwa, and there has been an increase in snare poaching in the region (Creel et al., 2018, 2024; Reyes de Merkle et al., 2024). While hippos are targeted by poachers for bushmeat in other parts of Africa (Nielsen and Meilby, 2015; Utete, 2020), the prevalence of hippo poaching in the Luangwa remains unclear. Data are also lacking on population vital rates for hippos, such as survival estimates across age and sex. Such data are valuable to conservation decision making (Ferraz et al., 2021; Johnson et al., 2010).

Despite the challenges, identifying regions with substantial hippo populations, such as the Luangwa River system, can serve important focal points for conservation efforts. By concentrating resources and management actions in these areas, we can maximise the effectiveness of conservation strategies and enhance the prospects for the persistence of relatively large hippo populations. Preserving the connectivity of long, free-flowing rivers is imperative (Grill et al., 2019), as disruptions such as diversions, irrigation, and damming can alter flow dynamics and reduce suitable freshwater habitats. The Luangwa River, recently recognised as a top candidate for additional protection in Zambia (Lehner et al., 2021), exemplifies this need. Any instream developments could fragment the main channel from its downstream continuity and completely destabilise the system, highlighting the importance of extending conservation efforts beyond Protected Areas to include entire river catchments.

Variation in the number of records to fulfil or surpass recent country-wide estimates demonstrates that accessible records of hippo distribution are inconsistent throughout the region. Notably, CITES (2022a) highlight that the IUCN estimate of 115,000–130,000 hippos across Africa is likely an underestimate and may be more appropriately in the range of 162,000–192,000 with some caveat given the limited reliability of count data. This increase is largely due to vast un-surveyed areas in the IUCN assessment and underestimates from commonly used survey methodologies (CITES, 2022a). Without a baseline of knowledge on the current numbers of hippos, the development of objective management decisions to allocate limited resources for conservation efforts may prove difficult.

The diversity of survey methods used to estimate hippo populations highlights potential shortcomings in current monitoring efforts. Aerial surveys (such as through the use of fixed wing aircraft), can quickly cover vast and remote areas, offering broad spatial coverage. However, aerial surveys can be costly and dangerous, and observer bias may not be accounted for. Aerial surveys not specifically focused on hippos, such as general wildlife surveys, may further contribute to undercounts, as they may not allow for enough time to deal with hippo submergence. Where aerial surveys are not possible, robust data on hippo populations can be derived from other approaches, including boat surveys (Chakuya et al., 2024) and walked transects (Kanga et al., 2011). However, these methods may be more labour-intensive and time-consuming, posing logistical and financial challenges in covering extensive areas. Innovative approaches for counting hippos may therefore be required to overcome current monitoring issues.

The recent application of Unmanned Aerial Vehicle (UAV) surveys (Fritsch and Downs, 2020; Inman et al., 2019; Inman and Leggett, 2022; Linchant et al., 2018) and remote sensing (Irvine et al., 2019) promise advancements in accuracy and efficiency, while offering opportunities for more consistent monitoring. Using combinations of survey methods may also enhance precision (Linchant et al., 2018), and future work is required to consider which approaches work together most effectively. Embracing advancements in survey methods and offering specialist training to increase accessibility to these, while striving for methodological standardisation, will improve effectiveness of conservation strategies and ensure sustainability of hippo populations.

Our database advances the current understanding of hippo distribution and abundance, underscoring the need for enhanced research efforts to sustain persistence of remaining populations. As hippo surveys continue to indicate population declines in some regions (Bempah et al., 2022; Chakuya et al., 2024; Fritsch et al., 2021), updating range maps to identify priority regions and populations may be vital. Maps play crucial roles in communicating with policymakers and development planners, as well as for planning conservation efforts (O'Connor et al., 2019). To enhance current range maps, there is a need for the investment of further resources and efforts in specific regions to conduct systematic surveys across broad scales.

Documentation of known hippo occurrences across southern Africa from 2000 to 2023 reveals that data on hippo distribution and abundance are geographically and temporally inconsistent. Where data are available, variations in survey methods contribute to discrepancies, and limit the accuracy of broad-scale population monitoring efforts, including those available through IUCN Red List. There is an urgent need for international collaboration, particularly in Transfrontier Conservation Areas, to collectively survey hippo populations using standardised techniques. Continued monitoring of hippo populations and consistent updates to range maps across the subregion to guide effective management strategies may be integral to the future persistence of this influential African megaherbivore.

In closing, we exhausted all possible avenues to obtain data here, but we recognise that our database may have omissions. Any species-specific population database remains a work-in-progress, and to this end, we encourage the IUCN SSC Hippo Specialist Group to extend this initiative and develop a spatial database of hippo population estimates and distribution across Africa.

CRediT authorship contribution statement

Hannah Lacy: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maria Beger:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Lochran W. Traill:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110878.

Data availability

The data used in this article is available in the supplementary material. For specific data requests, please contact the corresponding data owners directly.

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