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On the role of (and threat to) natural history museums in mammal conservation: an African small mammal perspective

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Abstract. The global environment is faced with growing threats from anthropogenic disturbance, propelling the Earth into a 6th mass extinction. For the world's mammals, this is reflected in the fact that 25% of species are threatened with some risk of extinction. During this time of species loss and environmental alteration, the world's natural history museums (NHMs) are uniquely poised to provide novel insight into many aspects of conservation. This review seeks to provide evidence of the importance of NHMs to mammal conservation, how arguments against continued collecting of physical voucher specimens is counterproductive to these efforts, and to identify additional threats to collecting with a particular focus on small mammals across Africa. NHMs contribute unique data for assessing mammal species conservation status through the International Union for Conservation of Nature's (IUCN) Red List of Threatened species. However, NHMs' contributions to mammal conservation go well beyond supporting the IUCN Red List, with studies addressing topics such as human impacts, climate change, genetic diversity, disease, physiology, and biodiversity education. Increasing and diverse challenges, both domestic and international, highlight the growing threats facing NHMs, especially in regards to the issue of lethally sampling individuals for the purpose of creating voucher specimens. Such arguments are counterproductive to conservation efforts and tend to reflect the moral opposition of individual researchers than a true threat to conservation. The need for continued collecting of holistic specimens of all taxa across space and time could not be more urgent, especially for underexplored biodiversity hotspots facing extreme threats such as the Afrotropics.

Key words: IUCN Red List, voucher specimen, Africa, next-generation (holistic) collecting, research ethics

There is little doubt that Earth is entering the 6th mass extinction (Ceballos et al. 2015), with terrestrial vertebrates being particularly affected by the pressure of anthropogenic change (Tilman et al. 2017). For birds and mammals faced with extinction, a suite of both indirect (e.g. habitat alteration and loss) and direct (e.g. hunting pressure) threats have been identified as major obstacles to their conservation (Tilman et al. 2017). Interestingly, and at odds with opinions often

voiced by critics (Minteer et al. 2014), collecting specimens for on-going and future research in collaboration with natural history museums (NHMs) is not one of these major threats (Rocha et al. 2014). In fact, NHMs have and continue to contribute to conservation of the world's mammals in a multitude of ways. This review, stemming from a talk given at the 13th Annual Meeting of the African Small Mammal Symposium (ASMS) held in Mekelle, Ethiopia in September 2019,



provides an attempt to highlight the many ways NHMs contribute to mammal conservation, with a particular focus on African small mammals. In addition to reviewing contributions made to mammalian conservation from NHMs, I discuss the difficulties facing such institutions and strive to highlight potential solutions to these obstacles. The value of NHMs and challenges facing these important institutions are highlighted using examples from Africa whenever possible, although examples from other countries are also referenced. Before diving in, I want to recognize the irony of a non-African writing this piece, but I hope my opinion is received in the good spirit in which I tried to deliver it and that the examples provided are reflective of the views of the global natural history community at-large.

A global tool in the fight to conserve mammals

When one thinks of animal conservation, and vertebrates in particular, a specific tool and organization critical in the fight to conserve Earth's biodiversity (Ceballos et al. 2017) tends to stand out above the rest: the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (Rodrigues et al. 2006). The IUCN Red List stands as *the authority* on the current conservation status of Earth's flora and fauna and is used by scientists and regulators alike to address challenges associated with conserving Earth's natural resources (Vié et al. 2009). In brief, the IUCN Red List uses a suite of five quantitative criteria to "Assess" the current conservation status of a particular species, resulting in an assignment

of that species to 1 of 9 Categories – Not Evaluated, Data Deficient, Least Concern, Near-threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, or Extinct (Vié et al. 2009). In addition to information pertaining to the five criteria, supporting information (SI) is required to accompany all assessments (IUCN 2012). The 13 pieces of required SI include information ranging from taxonomic data to the names and contacts of those responsible for the assessments (Table 1). Although such information often relies on published studies in the literature, for many taxa, i.e. small mammals, a good deal of the information used to assess individual species' conservation status stems from data collected for and housed within the world's NHMs (Stanley et al. 2005, Jones et al. 2009, Butchart & Bird 2010, Brummitt et al. 2015).

Before continuing, an explicit definition of what constitutes a "small mammal" must be provided. In the context of this piece a small mammal refers to any extant mammal species of the orders Afrosoricida, Carnivora (≤ 15 kg), Chiroptera, Eulipotyphla, Hyracoidea, Lagomorpha, Macroscelidea, or Rodentia found in continental Africa and the islands of Madagascar, Mauritius, and Réunion (Table 2).

Across African small mammals, 17% (192 species) face some risk of extinction with two recorded extinctions – *Pteropus subniger* (Kerr, 1792) from Mauritius and Réunion and *Cryptoprocta spelea* Grandidier, 1902 from Madagascar – to date. The Afrosoricida contain the highest percentage of

Table 1. List of 13 kinds of Supporting Information (SI) used in assessing a species conservation status for the IUCN Redlist. Boldfaced topics indicate categories that rely substantially on information provided or supported by specimens housed in natural history museums.

1. **Scientific Name (including synonyms)**
2. **Higher Taxonomy**
3. **Taxonomic Authorities**
4. IUCN Red List Category and Criteria
5. Rationale for Red List Assessment
6. Data for Parameters Triggering Red List Criteria
7. **Countries of Occurrence**
8. **Geo-referenced Distribution Data**
9. Direction of Current Population Trend
10. Freshwater, Terrestrial, or Marine Classification
11. **Suitable Habitats Utilized**
12. Bibliography
13. Names and Contact Details of Assessors and Reviewers (at least one)

Table 2. Summary of African small mammal diversity and conservation status based on the IUCN Red List, accessed 19 February 2020.

Order	Total species	Extinct/EX wild	Threatened species*	Data deficient
Afrosoricida	55	0	19	4
Carnivora	83	1	22	3
Chiroptera	305	1	49	65
Eulipotyphla	177	0	44	39
Hyracoidea	5	0	1	0
Lagomorpha	15	0	2	0
Macroscelidea	19	0	2	4
Rodentia	468	0	53	83
Totals	1,127	2	192 (17%)	198 (17.6%)

* Includes all species classified as one of the following Near Threatened, Vulnerable, Endangered, or Critically Endangered.

species facing extinction, with 35% (19 species) falling into one of four conservation categories. Of the 1,127 species of African small mammals, nearly 18% (198 species) fall within the category of Data Deficient, indicating there is not enough information available to make an accurate assessment of their conservation status.

A major reason that so many species of small mammal remain Data Deficient can be attributed to the difficulty in studying them due to several aspects of their behaviour; small mammals are often nocturnal, cryptic, difficult to observe directly, and best studied using specialised trapping that is labour intensive and expensive (Wilson et al. 1996). One of the best tools for studying small mammals can be found in the drawers and cabinets of the world's natural history museums. NHMs contribute to the conservation of small mammals in a multitude of ways, including direct contributions to the IUCN Red List's supporting information.

NHMs contributions to IUCN Red List

Taxonomy

For better or worse, conservation is most directly applied at the species level (Vié et al. 2009) and many conservationists have pointed to the importance of "names" when it comes to conserving biodiversity (Dubois 2003). In his seminal book chapter on the integration of systematics into conservation of biodiversity, Barrowclough (1992) aptly points out: "A prerequisite to making any decisions concerning the preservation of populations, species, or higher taxa is knowledge of their existence", in other words, we cannot conserve that which we do not know. Although mammals are often touted as the best known group of animals on the planet, their taxonomy remains in flux (Burgin et al. 2018), even

for charismatic megafauna like African bovids (Gippoliti et al. 2018).

The most recent systematic assessment of global mammal taxonomy found an increase of 1,079 recognized species of mammals since 2004, with a long-term global trend of around 25 new species described per year, resulting in a total of 6,495 species for the Class Mammalia (Burgin et al. 2018). Across biogeographic regions, the Afrotropics was second only to the Neotropics when it came to the greatest number of currently recognized species (1,572 species) and the most newly recognized species (357 species – 158 de novo and 199 split). Taxonomic changes across the Afrotropics and continent in general are especially frequent for African small mammals (Huntley et al. 2019).

Addressing the number of newly described mammal species found in continental Africa and all surrounding islands, including Madagascar, Hoffmann et al. (2009) documented 138 newly described mammal species during 1989-2008. Although primates, with 47 new species, had the highest number for a particular mammalian order, combining the five orders representing small mammals, as defined in this paper, yielded 89 new species, or 64.5% of the total number of newly described species for the region. Focusing again on the Afro-Malagasy region, Taylor et al. (2019) used a four-criterion system to assess the number of newly described species of rodents and bats since 1989. Building on the summary presented in Hoffmann et al. (2009), they found support for an additional 15 new species of rodents and 32 new species of bats described during 2009-2017 (Taylor et al. 2019). A majority of these species described since 2009 are restricted to Afro-montane habitats, placing them at a higher extinction risk and



requiring substantial conservation efforts to ensure their persistence into the future (Taylor et al. 2019).

In contrast to both of these papers, which retroactively summarized new species already described, Fisher et al. (2018) used models to predict the number of mammal species remaining to be discovered and found that together with the Neotropics, the Afrotropics represented the region with the most undescribed species with a predicted 122 undiscovered species of mammals (Fisher et al. 2018). Such a number does not seem unrealistic when one considers the number of unique evolutionary lineages awaiting description (Corti et al. 2005), or groups of mammals inhabiting this region with grossly underestimated species diversity, such as shrews (Dubey et al. 2007). In fact, in this very issue of the *Journal of Vertebrate Biology*, four new species of small mammals from Ethiopia, two shrews of the genus *Crociodura* Wagler, 1832 and two rodents of the genus *Stenocephalemys* Frick, 1914 have been described for the first time (Konečný et al. 2020, Mizerovská et al. 2020). These new species result from recent expeditionary work in Ethiopia and until such work was completed, were not represented in NHMs, much less known to science.

Countries of occurrence

Reliance on museum specimens as a source for known occurrence in a particular country is best illustrated from a personal example involving the Ethiopian genet *Genetta abyssinica* (Rüppell, 1836) in the country of Djibouti (Ferguson et al. 2019). Known from only 19 museum specimens, *G. abyssinica* was listed as occurring in the country of Djibouti based on a single specimen in the Muséum National d'Historie Naturelle (MNHN) in Paris. The only locality data associated with this specimen was "Djibouti", which although a small country, limits the inferences that can be drawn from the provenance of this single specimen. In 2016, as part of a collaborative team of scientists working to assess the mammal diversity of Djibouti's Forêt du Day, we had the chance to trap this rarely recorded species. Sacrificing the single individual we caught provided the first record for the country in over 60 years, GPS coordinates of its location and a new habitat type added to its niche, the only available post-cranial material for comparative morphological work, and genomic-quality tissue samples and parasites. The presence of a permanent and verifiable voucher specimen is particularly important in this case given the novel

location and potential for misidentification of this species (Gaubert et al. 2009).

Geo-referenced distribution data

Continuing with small carnivore examples, Gaubert et al. (2006) used data exclusively from natural history museums to document range expansions, potential geographic barriers, and habitat use for three of the rarest species of genets inhabiting Africa's lowland rainforests. As was the case with these genets and for many other African small mammals, the localities and dates associated with vouchered specimens in NHMs provide some of the only large-scale, verifiable data on native distributions of organisms, allowing scientists to assess how such distributions have changed across time (Page et al. 2015). The use of museum specimen data has been particularly instrumental in the emergence and expansion of predictive ecological niche or species distribution modelling (Anderson 2012), especially in the case of cryptic and hard-to-observe species such as African rodents (McDonough et al. 2015).

Suitable habitats occupied

As illustrated with the Ethiopian genet (Ferguson et al. 2019), knowledge about the habitats used by small mammals often rely on ancillary data associated with museum vouchers. The increased efforts to digitize collectors' field notes and data from specimen tags will certainly continue to enhance the use of NHMs to detect changes in species' natural histories over time and space (Graham et al. 2004). Although examples using African small mammals seem limited, use of habitat data from museum tags have been used to help clarify species identities from historical records of large, South African mammals (Boshoff & Kerley 2010). In some cases, the presence of a voucher specimen without associated habitat data can even be used to infer the presence of a particular habitat in a historical context, as demonstrated with museum vouchers of a North American habitat specialist, the pygmy rabbit *Brachylagus idahoensis* (Merriam, 1891) (Larrucea & Brussard 2008).

NHMs contributions to mammalian conservation at-large

Although critical to aspects of the IUCN Red List, NHMs and their cases of specimens contribute to mammalian conservation in a variety of ways (Drew 2011, Cook & Light 2019). In an attempt to highlight such contributions in a cohesive



manner, with a particular focus on African small mammals, references were gathered using Google Scholar for the following six categories: human impacts, climate change, genetic diversity, disease, physiology, and biodiversity education. A general search was conducted using the following terms: “museum specimen mammal Africa” plus the exact phrase of the six various categories (e.g. human impacts). In addition to these African small mammal examples, other papers relevant to the topic and involving mammals were included. Clearly this does not represent a comprehensive literature review but instead is meant to provide select examples highlighting the contributions of NHMs to each of the six categories.

Human impacts

The temporal, spatial, and taxonomic snapshots of Earth provided by museum specimens make them particularly useful for documenting the impacts of these environmental changes, including environmental contamination and emerging infectious disease (Schmitt et al. 2019). In fact, the millions of museum specimens stored around the globe provide unparalleled access to data that can potentially transform the field of global change biology (Meineke et al. 2019).

For African small mammals, two recent papers highlight how museum specimens have enabled complex studies of human impacts on the environment. Askay et al. (2014) used metrics of fluctuating asymmetry and body condition from museum specimens collected from East Africa’s Albertine Rift Valley to examine the impacts of environmental stressors, in the form of anthropogenic habitat change, on the brush-furred mouse *Lophuromys aquilus* (True, 1892). Using museum records from African expeditions that comprehensively sampled mammals during the early 1900s, Tóth et al. (2014) demonstrated a decrease in beta-diversity across six protected areas in Kenya. The study found support for decreased uniqueness among the six protected areas over time due to site occupancy from species adapted to human-inhabited areas (Tóth et al. 2014).

Examples of human impacts on the evolutionary ecology of non-African small mammals include the impacts of the reduction of prairie habitat on deer mouse *Peromyscus maniculatus* (Wagner, 1845) and *P. leucopus* (Rafinesque, 1818) distributions in the Chicago-land area (Pergams & Nyberg 2001) and shifts in skull sizes in insectivorous bats *Pipistrellus*

kuhlii (Kuhl, 1817) in response to foraging under artificial lights in Europe (Tomassini et al. 2014).

Climate change

The broad taxonomic and geographic holdings of NHMs resulting from repeated collecting over long periods using a variety of methods provide a unique dataset for studying biotic responses to climate change (Pyke & Ehrlich 2010). Although not without limitations, these datasets create a unique opportunity for collaborations between NHMs and global change biologists to address one of the most pressing questions facing biologists today: how biota will respond to anthropogenic climate change (Johnson et al. 2011).

One example addressing the impacts of climate change on African small mammals is the work on vlei rats in the genus *Otomys* F. Cuvier, 1824 in South Africa (Nengovhela et al. 2015). Examining cranial size in two species of *Otomys*, Nengovhela et al. (2015) demonstrated rapid morphological change over a 100 year period in response to warming temperatures associated with climate change. Another study using predictive niche modelling for forest shrews in the genus *Myosorex* Gray, 1837 based on records from museum specimens resulted in their uplisting on the IUCN Red List due to threats of future climate change scenarios (Taylor et al. 2017). Other examples studying the impacts of climate change on African small mammals tended to focus on the impacts of Plio-Pleistocene climate change (McDonough et al. 2015, Bryja et al. 2017, Mazoch et al. 2018) instead of changes during the Holocene and Anthropocene, although a recent paper using data from bat specimens across southern Africa found no effect of future climate change on losses of phylogenetic diversity when compared to random extinction simulations (Pio et al. 2014).

Numerous studies of the impacts of climate change on small mammals in North America have relied on museum specimens to infer shifting ranges across time (Wiens 2016), facilitating predictions regarding the impacts of anthropogenic climate change for all terrestrial mammals in the United States and Canada (McCain 2019). One of the best examples is the resurvey of Joseph Grinnell’s early 20th century trapping efforts for small mammals in California’s Yosemite National Park (Moritz et al. 2008). Other studies using museum specimens to track small mammal responses to climate change include the work of Myers et al. (2009) in the



Great Lakes region and additional studies from California (Rowe et al. 2015).

Genetic diversity

Museum specimens in studies of genetic diversity provide one of the best examples of the hidden value of these archives; being collected for historically relevant reasons, early collectors had no idea of the value the specimens they prepared would yield in the form of historic or “ancient” DNA. With the advent of Sanger sequencing and Next-Generation DNA sequencing (NGS), obtaining useful DNA from museum specimens of mammals has become a common-place request for NHMs (McDonough et al. 2018). Uses of such material in conservation biology are diverse but have tended to focus on population genetics across time (Wandeler et al. 2007).

Nearly all examples using museum specimens to examine losses in genetic diversity through time or within a specific population or location in Africa have targeted larger, more charismatic species. Whitehouse & Harley (2001) compared genetic diversity in a population of elephants *Loxodonta africana* (Blumenbach, 1797) in Addo Elephant National Park using modern and museum specimens and found a loss of two microsatellite alleles over time. Dures et al. (2019) compared museum specimens collected during the late 19th and early 20th century to samples from modern, extant populations of African lions *Panthera leo* (Linnaeus, 1758) and argued for a rapid decline in allelic richness associated with the rise of European colonialism in the area. Van der Valk et al. (2019) used NGS of century-old museum specimens of eastern lowland *Gorilla beringei graueri* Matschie, 1914 and mountain gorillas *Gorilla beringei beringei* Matschie, 1903 to demonstrate the genomic consequences associated with small population size. Although not explicitly focused on conservation genetics, the list of systematic and biogeographic papers of African small mammals using historical samples from museum specimens is extensive, with examples from the following orders provided just to highlight a few: Afrosoricida (Olson et al. 2004), Carnivora (Gaubert et al. 2005), Chiroptera (Goodman et al. 2017, Demos et al. 2019), Eulipotyphla (Jacquet et al. 2015), Lagomorpha (Lado et al. 2019), Macroscelidea (Dumbacher et al. 2012, Carlen et al. 2017), and Rodentia (Coetzer & Grobler 2018).

Outside Africa, historic and modern specimens collected during small mammal resurvey efforts

in California’s Yosemite National Park, USA were used to address the impacts of climate-change on genetic diversity in two populations of alpine chipmunks *Tamias alpinus* Merriam, 1893 (Rubidge et al. 2012). Expanding on these results, Bi et al. (2019) used exon sequencing of modern and historic museum specimens to uncover signatures of population genetic fragmentation through time for the Alpine adapted chipmunk (*Tamias alpinus*) not observed in a co-distributed species *T. speciosus* Merriam, 1890. In an example using a North American small carnivore, Perrine et al. (2007) compared historic samples of native populations of high-elevation dwelling red foxes *Vulpes vulpes* (Linnaeus, 1758) to exotic populations living in low-elevation habitats, finding support for the genetic distinctiveness of the native population.

Disease

Diseases of wild animals are capable of causing serious population declines in small mammals, as has been recently observed in the case of white-nose syndrome in North American bat species (Foley et al. 2011). Although novel infectious diseases have been shown to cause extinction in some vertebrate groups such as amphibians (Lips 2016), examples in mammals remain relatively scarce (Pedersen et al. 2007). The first unequivocal case of disease-caused extinction in mammals relied on museum specimens from the Christmas Island rat *Rattus macleari* (Thomas, 1887) collected pre- and post-invasion by a non-native rat *Rattus rattus* (Linnaeus, 1758) carrying a trypanosome parasite (Wyatt et al. 2008). Museum specimens thus provide another mechanism for investigating the impacts of anthropogenic change on emerging infectious disease relevant to both conservation and human health (Schmitt et al. 2019, Cook et al. 2020).

Given the important role wild small mammals may have in zoonotic disease transmission across Africa (Han et al. 2015, 2016, Diagne et al. 2017), it was surprising to find so few examples that relied on historic specimens housed in museums for disease investigations (DiEuliis et al. 2016). The most clear cut example involved screening over 100 museum specimens of African rope squirrels *Funisciurus Trouessart, 1880* for monkeypox virus, a study which resulted in moving evidence of monkeypox infections in host species back almost half a century earlier than originally proposed (Tiee et al. 2018). The rest of the studies found were mostly related to active field surveillance for detection of reservoir species of Ebola haemorrhagic fever virus



(Leirs et al. 1999). Concerted efforts by various teams to discover the reservoir host of EHFV could have been improved by the presence of reference collections from wildlife reservoirs which would both allow for refined searches of putative hosts (Leirs et al. 1999, Olson et al. 2012) as well as retroactive screening of previously collected samples (Schoepp et al. 2014).

Hantavirus Pulmonary Syndrome (HPS), caused by a novel hantavirus (Bunyaviridae), subsequently named Sin Nombre virus, or SNV (Nichol et al. 1993), provides one example of the power of NHM specimens in fighting emerging zoonotic diseases (Yates et al. 2002). With small rodents suggested as the primary reservoirs, researchers took advantage of extensive rodent collections housed in institutions like the Museum of Southwestern Biology and used these specimens to determine the evolutionary origins of the virus, how it spread among rodent populations, and develop predictions of new outbreaks among humans (Yates et al. 2002). The availability of a regionally important collection of holistic museum specimens that spanned temporal and environmental gradients certainly facilitated a more rapid and effective response to this lethal pathogen (DiEuliis et al. 2016).

Other examples involving the use of museum specimens in documenting the impacts of disease with a conservation angle include tracing the evolutionary dynamics of retroviruses in koalas (Ávila-Arcos et al. 2013) and the documentation of the occurrence of white-nose syndrome in a bat specimen collected from France in the early 20th century (Campana et al. 2017). As novel technologies continue to develop, museum specimens will continue to provide a unique opportunity for studying pathogens in wild mammals, as was recently demonstrated in a study that used DNA metabarcoding to characterise small mammal helminth communities across space and time (Greiman et al. 2018).

Physiology and anatomy

Impacts of anthropogenic disturbance are often registered in the physiological responses animals have to such perturbations, which can manifest themselves as direct threats to the conservation of such populations (Wikelski & Cooke 2006). Although much of the work on conservation physiology has focused on use of non-invasive assays of wild or captive mammals, museum

specimens offer a unique window into the impacts of stressors on wild animals as well as a source for insightful information on life histories of threatened mammal populations (Crumsey et al. 2019).

The most clear-cut example from Africa, albeit not from a small mammal, involves the use of museum specimens of the endangered addax *Addax nasomaculatus* (de Blainville, 1816) to derive insights into key life-history traits related to their conservation (Marín-Moratalla et al. 2013). Using long bones from three captive and two wild specimens of addax, Marín-Moratalla et al. (2013) used bone histology to determine age at sexual maturity and growth rates, two life-history traits that are correlated with extinction risk in mammals (Purvis et al. 2000). The importance of dental (odontochronology) and bone (skeletochronology) microstructure in assessing mammalian evolution and ecology, including the impacts of stress on individuals, certainly adds value to the bones of all mammals housed at NHMs (Hogg 2018). The use of hair cortisol levels also has great potential in measuring stress responses in small mammals stored in NHMs, even in the presence of historical chemical treatments of such as arsenic (Acker et al. 2018). Other examples from small mammals in Africa were more focused on direct assessments of physiological conditions, such as hearing organs in gerbils (Lay 1972) or brain size in carnivores (Sheppey & Bernard 1984), than in understanding how these physiologies related to conservation.

Biodiversity education

This last category lies at the core of many NHMs mission statements: implementation of biodiversity education (Drinkrow et al. 1994). Biodiversity education at NHMs can represent an array of goals ranging from education of the general public to specialised training of graduate students and taxonomic professionals (Wheeler & Miller 2017). NHMs are often best placed to implement such programs and simply having a NHM present in a community has been shown to positively impact conservation-relevant outcomes both directly, through site and species management, and indirectly through research, education, and policy statements (Ballard et al. 2017).

Resident experts in NHMs are often responsible for generating and publishing key works on the natural history, ecology, and systematics of mammals. Production of a number of these benchmark works from scientists working in



southern African museums provides a great example of their contribution to conservation through information dissemination in a publicly accessible framework (Herbert 2000). South African museums in particular appear to place a large emphasis on education in their mission statements, in part due to the fact that the public's perception of such museums is based largely on their education and service activities (Drinkrow et al. 1994). An example from South Africa involving a small animal, but not a small mammal, was demonstrated using ant monitoring research to raise awareness of biodiversity conservation in non-traditionally served communities (Braschler et al. 2010). Although not explicitly mentioned by the authors, Central Africa's growing interest in evolution and conservation education at the collegiate level could also benefit from the establishment of regional museums, especially when combined with university programs located in close proximity to important conservation areas (Anthony et al. 2015). The age of digitization provides a unique opportunity for such regional institutions to join what is being called the "Global Museum", providing opportunities for training in biodiversity informatics, GIS, and computer science, all of which go hand in hand with modern NHMs (Bakker et al. 2019).

In North America, digitization efforts have been used to provide access to communities for whom collections have often been out of reach, providing opportunities to expand diversity in biodiversity conservation (Drew 2011). Multiple examples of directly integrating NHMs into undergraduate education have been developed which could serve as models for other countries (Cook et al. 2014, Hiller et al. 2017, Monfils et al. 2017) as well as studies on the effectiveness of various education programs such as school tours (Cox-Petersen et al. 2003).

Why do we need continued collecting?

Hopefully the aforementioned examples of using museum specimens to assist mammal conservation are evidence enough for the need for continued collecting. However, one can easily point to the emphasis on *historically collected material* from said examples, raising the question of why do we need to continue to collect *new material* for NHMs? Although there are many reasons for continued collecting and deposition of specimens into NHMs (Goodman & Lanyon 1994, Peterson et al. 1998, Bates et al. 2004, Rocha et al.

2014, Paknia et al. 2015, Malaney & Cook 2018), see Patterson (2002) for a thorough synopsis for mammals, four reasons stand out: (1) specimens are the foundation for formal species descriptions and we are still discovering and describing new species of mammals at a rapid rate, (2) next-generation and holistic collections facilitate novel and interdisciplinary studies, (3) certain lines of research are impossible without freshly collected specimens, and (4) NHMs provide quality sources of information for addressing future global change.

Specimens and species descriptions

According to recent estimates, nearly 86% of the predicted 6.5 million species of terrestrial eukaryotes inhabiting Earth and 91% of the 2.2 million marine species await formal description (Mora et al. 2011). Although a majority of these undescribed taxa are likely to have small limited distributional ranges and live in less-explored areas (Mora et al. 2011), even charismatic and well-studied groups, such as mammals, remain grossly underestimated (Burgin et al. 2018, Fisher et al. 2018) often with direct consequences for critical ecosystem services (Ceballos & Ehrlich 2009). Underestimates of Earth's species richness means that recent (Anthropocene) extinctions may be up to twice as large as the current number recorded (Tedesco et al. 2014), supporting the fact that many species have become extinct even before we knew they existed (Mora et al. 2011). Formal descriptions of species requires a combined workforce of trained taxonomists (Pearson et al. 2011) and physical specimens (Ceriaco et al. 2016), both of which represent the cornerstones of NHMs. In spite of their critical role in describing Earth's biodiversity, NHMs are faced with growing criticism and lack of support (Cotterill & Foissner 2010), limiting their ability to describe species before they disappear (Pinheiro et al. 2019). This situation is particularly troubling in species-rich developing countries, where the lack of well-maintained NHM infrastructure represents an additional bottleneck to biodiversity exploration (Paknia et al. 2015).

Next-generation (holistic) collecting

Mammal specimens collected in 2020 go well beyond the classic "skin and skull" preparations of the late 19th and early 20th century, although these preparations still constitute an integral part of modern collecting efforts. These next-generation collections provide material for studying complex biological interactions (Schindel & Cook 2018) including the natural history of hosts and parasites



(Cook et al. 2016, Malaney & Cook 2018). Although the collection of these additional samples and data add time to specimen preparation in the field, they provide a unique set of interrelated data for addressing a variety of questions that remain unanswerable in the absence of newly acquired specimens collected under this framework. The power of new collections are particularly enhanced when NHMs partner with scientists in other disciplines prior to collecting, as illustrated by partnerships between NHMs and ecologists (Morrison et al. 2017) and disease biologists (Dunnum et al. 2017, Cook et al. 2020).

Studies requiring freshly collected specimens

Simply put, there are certain kinds of studies that are not possible without active collection of new mammal specimens, such as the holistic collection of hosts and their associated parasites; Galbreath et al. (2019) provide a step-by-step process for collecting and preparing holistic mammal specimens in relation to endo- and ectoparasite studies. Morphological studies of detailed anatomical features such as muscle fibre architecture in small mammals are often facilitated by fresh or frozen specimens (Ercoli et al. 2015, Gaudin & Nyakatura 2018). Transcriptome data, or expression studies, often require lethal sampling of a representative pool of individuals for effective sampling of fresh tissue types and characterization of their associated mRNA signatures (Hoffman et al. 2013). For example, a study examining kidney transcriptomes in the long-haired mouse *Abrothrix hirta* (Thomas, 1837) required lethal sampling of 16 wild-caught individuals (Valdez et al. 2015), although opportunistic sampling can provide an alternative source of tissues from highly endangered species (Hoffman et al. 2013). Collaborations between molecular biologists and NHM personnel can provide a unique opportunity for targeted collections of specimens for integrative studies, as was illustrated using a recent collection of bats in Guatemala (Phillips et al. 2012). Freshly collected tissues with associated vouchers can also provide a source of high-quality genomic DNA for non-model organisms that are rarely kept in captivity (Wong et al. 2012), as is the case with most African small mammals.

NHMs as time capsules

The millions of animal specimens deposited in NHMs provide an unrivalled data set for addressing how anthropogenic disturbance affect Earth's biodiversity and natural resources

(Meineke et al. 2019). These specimens span decades and sometimes centuries, providing unique data sources for revealing patterns not visible with other kinds of information (Meineke et al. 2019). Despite the growing threat of budget cuts and other institutional challenges, NHMs are still the best-equipped institutions for processing and housing these kinds of long-term datasets; such institutions are designed to archive data to ensure their availability in perpetuity, thereby minimizing the risks associated with data linked only to the careers of individual researchers. Unfortunately, limited investment in staff, infrastructure, and efforts for continued collecting at NHMs is creating a large gap in our future abilities to understand patterns of global change, especially for mammals (Malaney & Cook 2018). Renewed efforts to collect "temporally deep, geographically extensive, and site-intensive collections of holistic specimens" (Malaney & Cook 2018) by NHMs is the only solution to avoiding the loss of this information, a tragedy that will be lamented not by scientists of today, but of those working a century from now (Grinnell 1910).

Barriers to (international) collecting

In light of the previous examples supporting the value of continued collecting, the next section discusses known barriers to collecting with discussions of potential mechanisms for overcoming these obstacles, with a particular focus on international efforts. Although not exhaustive, major barriers to collecting include: opposition to killing, nationalism, bio-piracy, permits, and safety and accessibility.

Opposition to killing

In his paper on the need for continued museum specimen collection, Patterson (2002) elegantly summarized the debate over whether or not to collect, stating: "Dividing scientists and the public alike, this question has generated much heat but little light." Individual reasons for opposing the killing of animals for deposition into NHMs can be subdivided into three major categories: ethics, conservation, and taxonomic.

Ethical reasons

The ethics of killing animals in the name of science is a complex issue that often rests on the morality of one sentient being harming or killing another sentient being (Bekoff & Hettinger 1994, Bekoff & Elzanowski 2010). Under this worldview, scientists



should be respectful of the “individual interests of sentient animals” and morally obligated to justify this behaviour in ethical terms (Bekoff & Elzanowski 2010). In an attempt to harmonize animal rights and environmental ethics, Warren (2017) argued for a pluralistic viewpoint that recognized that animals have rights but that these rights are not the same nor equal to those of autonomous moral beings, i.e. humans.

NHM scientists are clearly bound by ethical guidelines on the treatment of animals, especially in regards to minimizing suffering (Sikes et al. 2016). NHM scientists are required to adhere to Institutional Animal Care and Use Committee (IACUC) principles of replacement, reduction, and refinement (Curzer et al. 2016). However, given the uniqueness of each specimen collected in terms of time, place, and future research use, replacement is not really an option and reduction can limit informative series for addressing broader questions (Curzer et al. 2016). In addition, multiple papers outlining ethical guidelines for justification of lethally collecting animals for NHMs have been written (Loftin 1992, Clemann et al. 2014). In the absence of a “true answer” to the question of to kill or not kill, these scientifically-based ethical guidelines should function as the guiding principles for continued collecting for NHMs, not an individual’s moral objection to the idea of killing individual animals.

Conservation reasons

Delving deeper into the scientific articles arguing for alternatives to lethal sampling for NHMs, a red herring begins to take shape in the form of an argument that killing animals is anti-conservation. The conservation argument to halt lethal collecting of wild mammals tends to be used to distract readers from the previously discussed ethical framework grounded in morality, not on genuine threats to animal conservation (Gippoliti 2018). Despite calls for limiting lethal sampling of mammals due to potential impacts on their conservation status (Russo et al. 2017, Waeber et al. 2017), these studies provide examples where collecting is thought to have played a significant role in the extinction of species for only non-mammalian taxa (plants – (Norton et al. 1994); fish, amphibians, and birds – (Rodríguez-estrella & Moreno 2006); amphibians and birds – (Minteer et al. 2014).

The argument that killing animals for NHMs is negatively impacting their conservation would

require information that demonstrates a lasting impact to population persistence in a given location or time. For the handful of published studies addressing the impacts of lethal collecting on small mammal populations, such risks do not seem to be backed up by empirical evidence. Based on their work on small mammal communities on the Sevilleta National Wildlife Refuge in New Mexico, USA, Hope et al. (2018) provided one of the most in-depth assessments of lethal collecting on small mammal diversity to date. With more than 30 species of non-volant mammals and a replicated, paired-comparative framework, i.e. paired plots with and without lethal sampling, their dataset of 13,000 mammal captures showed little to no effect of removal sampling on estimates of both species richness and abundance over a 7-year sampling period. Furthermore, no rare species were lost from the system and in the removal plots, rarer species were captured more frequently, a pattern also recorded for small mammal communities in Chile (Patterson et al. 1989).

In Africa, a study by Nicolas et al. (2003) in two African tropical forest sites found no significant effect of lethal sampling using removal pitfall trapping on shrew species diversity or density. Their work, conducted in two localities, one in the Central African Republic (1999–2000) and the other in Gabon (2000–2001), during seasons with comparable rainfall also showed the cumulative number of shrews trapped did not decline over time. In southern and east Africa, the ECORAT (Development of Ecologically-based Rodent Management for the Southern African Region) project compared the effectiveness of lethal trapping on rodent populations of four major agricultural pest species, *Rattus rattus* (Tanzania), *R. tanezumi* Temminck, 1844 (Eswatini), and *Mastomys natalensis* (Smith, 1834) and *Gerbilliscus leucogaster* (Peters, 1852) (Namibia) between communities implementing daily kill trapping to those not using any traps (Taylor et al. 2012). It took an effort of 100 trap nights per day per community over a year’s time, totalling 73,000 trap nights, to affect populations of these major pest species, reducing relative rodent populations by 48% (Swaziland) and 63% (Namibia) when compared to communities without lethal trapping (Taylor et al. 2012). Such trapping efforts far exceed those of a typical museum collecting trip. For example, recent collecting trips to Ethiopia, Tanzania, and the Democratic Republic of Congo resulted in 6,273 trap nights over a month long-period with



472 small mammals (349 rodents and 123 shrews) captured (Craig et al. 2020), 2,055 trap nights over a 10-day period resulting in 234 captured small mammals (Stanley & Foley 2008), and 4,036 trap nights over nine months spread across a three-year period resulting in 353 captured mammals (Doty et al. 2017), respectively.

Although not comprehensive in their geographic scope or taxonomic coverage, these studies provide some data on the impacts of lethal collecting on small-mammal populations. Even in the presence of persistent, and what some might consider intensive trapping pressure, impacts to small mammal communities and their conservation status proved negligible or non-existent. Additional studies from different regions of Africa on a variety of taxa would help to provide the necessary data to evaluate the claim that lethally sampling small mammals has the potential to provide additional threats to the conservation of these species.

One additional side note regarding the conservation argument is the fact that papers discussing the impacts of lethal collection on the conservation status of animals seem to focus their concerns solely on NHMs. This observation is made despite the fact that incidental mortalities occur across many other fields in the life sciences (Putman 1995, Jon et al. 2006, Waudby et al. 2019), although reporting of such data are not commonplace, especially for small mammals (Lemckert et al. 2006). In fact, both evolutionary (Peterson et al. 2007, Pleijel et al. 2008) and ecological (Bortolus 2008, Turney et al. 2015) research have been criticized for failing to voucher study animals, not citing the disposition of collected specimens (McLean et al. 2015), or even discarding specimens collected during survey work (Sullivan & Sullivan 2013, Cook et al. 2016). Hope et al. (2018) argued that all biodiversity scientists should practise responsible accessioning of collected specimens, experimental mortalities, and voucher specimens with such practices supported by the scientific community and supporting institutions (Winker et al. 2010, Turney et al. 2015, Ward et al. 2015).

One example from Africa involves the collection and deposition of mountain gorilla (*Gorilla beringei beringei*) skeletons from Rwanda (McFarlin et al. 2009), a resource that has provided information vital to understanding gorilla evolution (McFarlin et al. 2013), behaviour (Galbany et al. 2016), and development (Ruff et al. 2013). Another example

from South Africa included the vouchering of more than 1,350 mole rats *Bathyergus suillus* (Schreber, 1782) as part of a mole rat eradication program at Cape Town Airport that resulted in at least four scientific publications on the biology of this small mammal (Hart et al. 2006, 2007, Bray et al. 2011, Montoya-Sanhueza & Chinsamy 2017). Other sources of specimens obtained from non-direct collecting efforts include zoos and aquariums, loss of entire habitats such as that resulting from flooding from dam formation (Ceríaco et al. 2014), roadway mortality (Bullock et al. 2011, Gippoliti et al. 2018), incidental mortality (Davenport et al. 2006), biocontrol efforts (Leirs et al. 1990), trophy hunting (Gippoliti et al. 2018, Dures et al. 2019), and conflict management (Tensen et al. 2018). Although such sources of specimens cannot replace the systematic efforts of NHM scientists entirely (Goodman & Lanyon 1994), they provide alternative sources of specimens in the absence of moral, conservation, or taxonomic conflicts.

Taxonomic reasons

The “right to life” argument (Warren 2017) certainly seems to play a role in the taxonomic-biased argument against killing mammals for NHMs. Under the right to life framework, a non-human animal’s right to live corresponds to their capacity for moral autonomy and reciprocity, which differs across the animal kingdom. With the majority of criticisms focused on collecting vertebrates (Rodríguez-estrella & Moreno 2006, Minter et al. 2014) with a particular focus on birds (Collar 2000, Bekoff & Elzanowski 2010, Winker et al. 2010) and mammals (Russo et al. 2017, Hope et al. 2018), it is clear that such “higher vertebrates” are given a higher right to life than other taxonomic groups (Warren 2017, Salvador & Cunha 2020).

For mammals, taxonomic bias is also commonplace. Mammal groups more closely related to humans, such as non-human primates (Dubois & Nemesio 2007), highly visible species, or those of economic importance (e.g. game mammals), are often prohibited from being collected (Moratelli 2014, A.W. Ferguson, pers. observ.). As an example, the collection of hoofed mammals (ungulates) across Africa was regularly undertaken in the early 20th century (Heller 1912), but is nearly non-existent today despite large numbers of such animals being taken for trophy hunting (Peter et al. 2007). This limited collecting of an entire taxonomic group has direct consequences for understanding the taxonomic boundaries and ecology of such



species (Gippoliti et al. 2018), a problem that could potentially be remedied through partnering hunting activities with regional or international NHMs.

A recent push to curtail collecting vouchers of bats is illustrative of the taxonomic bias argument, with attempts to equate all bats with charismatic species with slow reproductive rates, such as elephants, in order to sway public opinion towards non-lethal methods (Russo et al. 2017). These blanket taxonomic-based rules ignore the individual ecology of species and geographic variability, for example assuming all tropical bats are as long-lived and reproductively limited as temperate species makes little ecological sense (Russo et al. 2017). Although equating all mammals to rodents is equally fallible, data indicate that even species considered taboo for collecting, such as small carnivores, can handle substantial individual losses and still persist at the population and landscape scale (Minnie et al. 2016, Barychka et al. 2019).

In South Africa, black-backed jackals *Canis mesomelas* Schreber, 1775, have faced intense and long-term persecution from private landowners yet still remain widespread and abundant (Thorn et al. 2013). In KwaZulu-Natal, a single landowner reported shooting 51 jackals in 2011, 39 in 2012, and 54 in 2013, suggesting that local jackal population numbers are high despite the numbers being shot annually, with new individuals recolonizing depleted areas quickly (Humphries et al. 2015). Other small carnivores, such as genets (*Genetta* spp.), also seem resilient when it comes to persecution as seen in the Servaline genet *Genetta servalina* Pucheran, 1855, which was more abundant in forests targeted for bush meat hunting than protected areas in the Udzungwa Mountains of Tanzania (Hegerl et al. 2015). In addition, many of these smaller carnivores maintain relatively high densities (Waser 1980, Kingdon & Hoffmann 2013), potentially minimizing the long-term impacts of low-level collecting efforts by scientists.

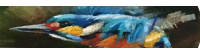
Nationalism, NAGOYA, and other impediments to collecting

The rise of global nationalism was partly to blame for the recent decision by scientists to push the Doomsday Clock 30 seconds closer to midnight (Lallensack 2017). Such drastic measures reflect the impacts political nationalism can have on advancing science, especially in regards to global issues such as climate change (Deese 2019). Advances in understanding the natural history of

the Earth's mammals have historically benefited from "network science" and been impeded by nationalist slants, as is illustrated in the case of natural history writings in Latin America (Duarte 2013). NHMs practicing multilateralism create benefits through increased productivity via collaborations and publications (Cook et al. 2014), shared resources (McLean et al. 2015), and infrastructure development in resource-limited countries (Paknia et al. 2015). Of course, the rise of scientific nationalism can be in response to imperialistic practices employed by foreign nationals, a practise of historical significance for NHMs (Budowski 1975) but one that has been acknowledged and is actively being combated by modern-day NHMs (Watkins & Donnelly 2005, Knell et al. 2007, Malhado et al. 2014).

In response to such imperialistic practices, and bio-piracy in particular (Rabitz 2015), the Convention on Biological Diversity developed the NAGOYA Protocol (NP), an international treaty that outlines procedures for access to genetic resources and benefit sharing that arise from the use of such resources (Watanabe 2015). Although the United States and Canada are not signatories to the NP, more than 196 countries or sovereign states have ratified the Protocol, resulting in significant impacts on international research, collections of biological materials, and management of existing collections (<https://learnnagoya.com>). Implementation of the NP has not been without problems, and many institutions, especially those in the US, are struggling to understand the direct implications of this protocol (Watanabe 2015). Fortunately, continued collaborations between local institutions and foreign NHMs are helping to navigate this difficult landscape in such a way that facilitates but does not entirely eliminate blockages to access of biological material (Fusi et al. 2019).

In a similar vein to the impacts of the NP on international collecting of scientific specimens (Neumann et al. 2018), the issuance of permits to transfer such material between countries also poses challenges to research efforts (Renner et al. 2012). Another US-centric example involves the treatment of various mammal groups by the Centers for Disease Control (CDC), which includes the designation of particular taxa, i.e. bats and non-human primates, as incapable of being rendered non-infectious using particular treatments such as fixation in formalin (42 CFR § 71.54 (f)(2)). In addition, the CDC currently recognizes 21 species



of bats, including 11 species found in Africa, as UN 2814, Category A, infectious substances, which requires shipping standards that are the same as transporting active viruses such as Ebola and rabies (IATA Classification 3.6.2.2.2.1) and storage in a Biological Safety Level-3 laboratory. Export permits from other countries are also challenging, especially when multiple institutions within a single country are thought to be authorized to issue such permits. Although not currently insurmountable, much of this bureaucratic red tape goes a long way towards impeding research progress and in the case of NHMs often limits which countries and what taxa they can work with.

One final consideration that limits exploration tied to NHMs on the international stage is safety and accessibility. Biases in collections are rampant within NHM mammal collections, for example most specimens of birds collected across continental Africa were heavily influenced by accessibility (Reddy & Dávalos 2003) and mammals are typically not surveyed in difficult to access areas such as mountaintops (Storz et al. 2020). NHM collections often tend to hold series of specimens with some level of geographic bias (Stoeckle & Winker 2009), which can be influenced by security and safety concerns (Daru et al. 2018) as well as the sporadic and researcher-led nature of collecting expeditions (Ward 2012). When it comes to these two issues, scientists are best advised to trust and adhere to in-country collaborator advice and to follow standard guidelines for field research in such areas (Hilhorst et al. 2016).

Next-generation specimen collecting

The 21st century has seen the growth of biological collections from individual fiefdoms into an integrated global network of samples and data with positive benefits for both science and humanity (Soberon 1999, Schindel & Cook 2018). It is within this context that the collection of museum specimens should be considered. The old days are gone. Modern NHMs seek to encourage and enhance collaborative research on Earth's biodiversity that facilitates local capacity, including the establishment of regional NHMs and training of in-country scientists. Modern NHMs spend millions of dollars to ensure the data housed within their walls are available for free through various open access platforms such as GBIF (<https://www.gbif.org/>), iDigBio (<https://www.idigbio.org/>), Morphosource ([\[morphosource.org/\]\(https://www.morphosource.org/\)\), IsoBank \(<https://www.isobank.org/>\), GenBank \(<https://www.genbank.org/>\), and MorphBank \(<https://www.morphbank.org/>\). Modern NHMs also continue traditional efforts of specimen collecting but with a modern twist that provides holistic specimens with ancillary data for interdisciplinary studies \(Schindel & Cook 2018\) while still performing their core function as taxonomic research resources \(Wheeler & Miller 2017\). Such collecting efforts are guided by stringent ethical guidelines and require justification that often supersedes that required of other disciplines where mortality is commonplace. These collecting efforts are not directed at causing the extinction of animals or contributing to the conservation crisis, but instead provide a vast network of people and institutions dedicated to using these specimens to deepen our understanding of Earth's biodiversity, conserve its flora and fauna, and educate those of us most responsible for its destruction.](https://www.</p></div><div data-bbox=)

Promoting a proactive approach to collecting in Africa

Critiques of specimen collecting for deposition into NHMs, especially for mammals and other vertebrates, recently appearing in the scientific literature (Minteer et al. 2014, Russo et al. 2017, Waeber et al. 2017) are actively met with scepticism and rebuttals (Rocha et al. 2014, Gippoliti 2018). However, taking a reactive approach inhibits our ability to limit the potential damage such critiques have on on-going efforts to document Earth's biodiversity, especially for species-rich areas and groups like African small mammals. Subjective limitations placed on collecting efforts, scepticism surrounding the goals of NHM researchers, and limited funding and support of NHMs continue to threaten efforts to document mammal diversity across parts of Africa, at a time when such diversity is being lost at an unprecedented rate (Huntley et al. 2019). Instead of restricting and limiting collecting efforts, we need to work towards promoting collecting efforts if we are to curtail this rapid extinction without description (Wheeler & Miller 2017).

In this regard, the African Small Mammal Symposium (ASMS) provides the perfect foundation for developing a collective group of like-minded scientists from across the globe to promote, coordinate, and implement 21st century collecting practices across the continent. Although extremely valuable for biodiversity discovery



(Monadjem et al. 2013, Peterhans et al. 2020), traditional expeditions can limit the ecological inference we can draw from museum specimens (Ward 2012). Given the limited resources available for NHMs, coordinating sampling efforts would go a long way towards maximizing our efforts to describe and conserve Africa's threatened mammal fauna, especially in a way that facilitates future studies of the impacts of anthropogenic disturbance. Encouraging studies on the impacts of scientific collecting on mammal populations of a variety of taxa, working with regulators to develop logical laws for managing such activities, and soliciting advice on the needs for and uses of specimens by in-country collaborators seem like a few initial avenues by which such a group could impact our field. Collaborating across disciplines will certainly be critical in promoting the responsible collection and deposition of specimens in NHMs (Ward et al. 2015), an area where the ASMS also has existing strengths.

Creating a consortium of interested scientists involved in collecting African mammals, or any museum specimens for that matter, could go a long way towards developing strategic mechanisms for coordinated sampling and deposition of voucher specimens for current and future studies. Developing such a network, even if only in digital space, has the capacity to facilitate active collecting of voucher specimens across the continent through shared experiences, coordinating sampling efforts, and creation of a unified voice in support

of collecting for NHMs. The existence of similar groups, such as the Middle Eastern Biodiversity Network (Krupp et al. 2009) and the African Small Carnivore Research Initiatives (ASCaRIs; <https://ascaris.org/>) provide precedence for such successful collaborations. Although not without its challenges, creating a collaborative effort to promote specimen collection for NHMs across Africa is an appropriate step towards promoting the importance of voucher specimens in understanding Earth's biodiversity and the growing threats humans pose to this irreplaceable natural resource.

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