Bridging the Research Gap between Live Collections in Zoos and Preserved Collections in Natural History Museums

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Zoos and natural history museums are both collections-based institutions with important missions in biodiversity research and education. Animals in zoos are a repository and living record of the world's biodiversity, whereas natural history museums are a permanent historical record of snapshots of biodiversity in time. Surprisingly, despite significant overlap in institutional missions, formal partnerships between these institution types are infrequent. Life history information, pedigrees, and medical records maintained at zoos should be seen as complementary to historical records of morphology, genetics, and distribution kept at museums. Through examining both institution types, we synthesize the benefits and challenges of cross-institutional exchanges and propose actions to increase the dialog between zoos and museums. With a growing recognition of the importance of collections to the advancement of scientific research and discovery, a transformational impact could be made with long-term investments in connecting the institutions that are caretakers of living and preserved animals.

Keywords: natural history collections, biological collections, biodiversity, zoos, aquariums

nimal collections are a repository of our A shared biodiversity and a valuable resource of scientific research and discovery (Dick 2017, Miller et al. 2020). Natural history museums hold preserved biodiversity collections and associated specimen and ecological data that have long been recognized as an invaluable and irreplaceable resource for biodiversity research and society (Johnson et al. 2011, McLean et al. 2016, Funk 2018, Nelson and Ellis 2019, Watanabe 2019, Lendemer et al. 2020, NASEM 2020). Zoos and aquariums (hereafter, we use *zoos* to refer to both zoos and aquariums) hold living collections of animals and associated data on life history, demographics, pedigree (genealogy), genetics, physiology, morphology, and behavior but are not typically recognized for their value for biodiversity research (see Zehr et al. 2014 for exceptions, but see Conde et al. 2019, NASEM 2020). Despite the potential for synergy that is apparent in the complementary and nonoverlapping specimen and data types held in zoos and natural history museums, formal partnerships between these two institution types are uncommon.

In the present article, we highlight how potential collaborations could enhance the value of both types of collections and advance collective missions of biodiversity conservation, research, and education. We begin by describing the types of collections and associated data held by each institution, with a particular focus on potential complementarity among types of specimens and data. We then describe benefits of collaboration to each institution type, highlight case studies of existing productive collaborations, and identify best practices for collaborations. We address logistical challenges to

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Table 1. Characteristics of collections and specimen data from natural history museums and zoos.		
Characteristic	Natural history museums	Zoos and aquariums
Collection focus	All organisms	Living animals
Collection size	500 million-1 billion	2.9 million (in ZIMS)
Species represented	Approximately 1.2 million	Approximately 16,000
Collection management software	EMU, Specify, Arctos, Symbiota	ZIMS, Tracks, Sparks, PopLink
Data accessibility	Online collection portals, data aggregators (e.g., iDigBio, GBIF)	By request only
Access to specimens	Standard loan request or collection visit	By request only
Contact person for specimen request	Info typically clearly stated on website, typically collection manager	Process idiosyncratic, varies among institutions (veterinarian, registrar, curator, research staff)

 Table 1. Characteristics of collections and specimen data from natural history museums and zoos.

integrating collection types, including needs in human and cyberinfrastructure and differences in cultures and values between institution types. We conclude with a list of action steps that institutions can take to link and leverage biological collections to advance biodiversity research.

Types of collections

Biological collections can take various forms and encompass different geographic and taxonomic scales.

Living collections and associated data in zoos. Institutions accredited by the Association of Zoos and Aquariums (AZA) hold roughly 800,000 living animals, primarily in the United States (table 1; AZA 2021b). These collections are strongly biased toward vertebrates and, in particular, birds and fish (Conde et al. 2019, Rose et al. 2019). Globally, zoos use a variety of collections software, with at least three million records digitized worldwide within the Species360 management system alone (Species360 2021), representing more than 21,000 species. In addition to living animals, zoos hold extensive records for each animal, starting with birth or transfer from the wild. Zoos record information on taxonomy, animal demography, and pedigrees, and they maintain longitudinal information on health, physiology, life history, behavior, and husbandry protocols used during the animal's life such as diet, veterinary treatments, and social groupings. As a part of routine health assessments, conservation breeding programs, or internal and external research projects, zoos periodically collect and preserve biological materials (whole blood, plasma, serum, DNA, gametes, etc.). Usually, zoos store these biological materials on site, either for the short or long term, depending on storage space and the conservation priority of the species. Typically, biobanks are not coordinated among institutions, but the recently launched European Association of Zoos and Aquaria biobank is an example of coordinated sample storage and coordination (Pérez-Espona 2021). In the event of an animal's death, the institution performs a thorough necropsy (Griner 1983, Terio et al. 2018), after which the physical specimen is usually destroyed through incineration or other means. The other biological materials associated with the animals are sometimes maintained and stored after the death of the organism; however, the storage and maintenance of these materials are highly variable and dependent on each institution's own policies.

For animals currently living within the collection, digital records are updated constantly using management software, such as ZIMS, Tracks, PopLink, or similar software (Cohn 2006, Faust et al. 2019). This information is continuously recorded during an animal's life, which is a major difference from records kept at natural history museums, and is maintained in perpetuity after the animal's death. Within AZA-accredited zoos, information typically is shared. This is necessary for the effective management of the entire captive population, which is seen as a single unit despite the fact that individual animals may be spread out across multiple institutions. Each individual animal has a global accession number and one or more local identifiers. Collection management software tracks detailed husbandry data, pedigrees, and medical records. For animals that have died, records are kept digitally within the management software or, in cases of historical records prior to digitization, are kept on paper.

As the mission of modern zoos has evolved into one of conservation and species preservation, the composition of living collections in zoos has changed over time to reduce the percentage of wild-caught individuals and, correspondingly, to increase the number of captive-born animals. Moreover, zoos have increased their focus on rare or endangered species in need of conservation efforts (Conde et al. 2013, Tapley et al. 2015) and have taken on larger numbers of nonreleasable animals from wildlife rehabilitation centers or confiscations from illegal trade (Fa et al. 2011). With each of these shifts, there is a corresponding effect on the scientific value of a collection's animals. For wild-caught animals, locality data may be of use, whereas captive-born animals can provide insights into genetics, health, and pedigree. Increased holdings of at-risk species that may be inaccessible elsewhere and rehabilitation of endangered species that are deemed "nonreleasable" provide the opportunity for research into animals that are in need of human intervention.

Preserved natural history collections in museums. Natural history museums hold roughly 500,000,000 to one billion biological specimens in US collections and three billion worldwide (table 1; NASEM 2020). These can be whole organisms (typically for smaller animals) or parts of those organisms (e.g., skins, skeletons, DNA, tissue, and associated ecto- and endoparasite samples). Natural history specimens typically include locality data, taxonomy, the collection date, and

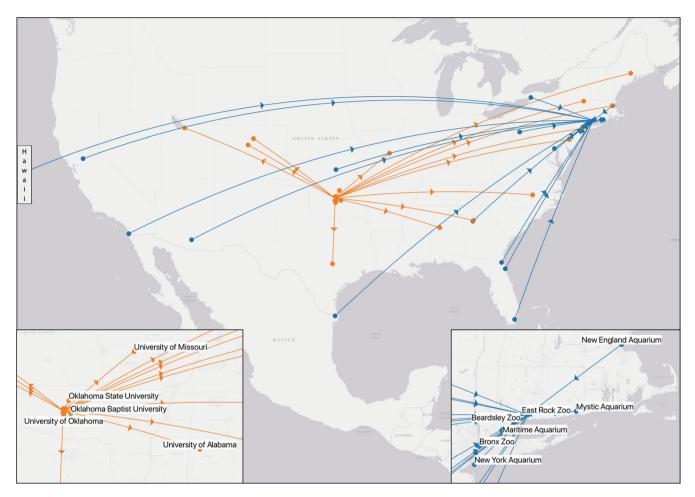


Figure 1. Zoos and museums can maintain robust sharing networks across the United States. The Yale Peabody Museum of Natural History has received specimens from zoos across the US (network shown in orange), whereas the Oklahoma City Zoo has shared samples and specimens with universities and museums (network shown in blue). Both zoos and museums can maintain robust local and country-wide networks.

the collector, as well as information on the treatment (i.e., the method of preservation) of the specimen. Generally, the information available on a specimen in a natural history museum begins with a collection event in the field that results in the attainment of specimens. Once the initial specimen information is obtained, it can then be extended through various lenses (e.g., archaeological, paleontological, geological, societal, or taxonomic). Because specimens are normally euthanized for natural history research, the collection of information during the life of the animal is generally limited. Typically, natural history collection records only represent a single instance in the time of the animal's life—specifically, the period just before its death. However, it presents a transition to research that requires preserved specimens.

Specimen data are held in a range of collection management software platforms, such as Specify, Arctos, EMu, and Symbiota. Unlike in zoos, specimen data are typically not shared across institutions through the collection management software itself. Rather, collection management software platforms frequently use a consistent metadata standard (e.g., the Darwin Core), which allows data interchange (Wieczorek et al. 2012). In recent decades, museums have dramatically expanded the digitization and accessibility of specimen data, which has profoundly enhanced the value of specimens for biological research (Nelson and Ellis 2019, Hedrick et al. 2020, Miller et al. 2020). Data aggregators, such as VertNet, GBIF, DiSSCO, and iDigBio, provide access to collection information across institutions and software platforms and have, along with local institutional web portals, made collection information and specimen details increasingly publicly accessible (Constable et al. 2010). The digitization of museum records is an ongoing process, but to date, less than 40% of the specimens in US collections are represented online, with a substantial portion of specimen information remaining to be digitized.

Benefits of collaboration

Closer collaboration between zoos and natural history museums has clear benefits to both parties (figure 1).



Figure 2. An Asian elephant from the Oklahoma City Zoo passed away from unknown causes (global accession no. 21517980). After the Museum of Osteology (also in Oklahoma) prepared the specimen as a skeleton and found affected and deformed molars, that diagnosis was determined to be the cause of death. The zoo now uses new dental monitoring techniques on its elephants because of this interaction with the museum. Photograph: Jennifer D'Agostino.

Benefits to zoos. Zoos typically do not have storage facilities or trained staff to curate preserved specimens in perpetuity. Instead, disposal of specimens is a logistical necessity and often a legal necessity, because of permitting or ownership requirements. As an alternative, if zoo specimens of high scientific value are deposited in natural history museums postmortem to become permanent specimens, this may lead to retrospective health information (figure 2) and genetic studies that could potentially contribute to assisted reproductive technologies that would benefit zoo collections in the future. Moreover, by extending the scientific lifespan of animals after death, zoos increase the usefulness of their collections and credibility as conservation-oriented and scientific organizations (figures 3 and 4; Miller et al. 2004, Loh et al. 2018). This is particularly important for zoos accredited by the AZA, which has placed increasing emphasis on the need to invest in scientific advancement through basic and applied research (Rose et al. 2019, AZA 2021a). Collaborating with museums and having museums report back to zoos (or the AZA) about the impact of linking zoo animals with museum specimens would help to raise awareness of the added value of depositing zoo animals in museums and to help zoos articulate to supporters how their animals go on to promote science and conservation after their death. This kind of reciprocal illumination could aid in producing more fruitful collaboration between these institutions.

Benefits to natural history museums. Museums receive clear benefits of expanding their collections with a deeper collaboration with zoos (figure 4). This includes not only whole

or part of the physical specimen but also eggs or embryos, DNA, tissue, and other biological samples and accompanying information. Because many animals in zoos represent species that are rare, endangered, or even extinct in the wild, collecting new specimens from the field could be difficult, impossible, or potentially unethical. Furthermore, zoo specimens are typically accompanied by a lifetime of data on demography, behavior, reproduction, health, husbandry, and more. For smaller collections or collections used primarily for teaching, the broad diversity of species held by zoos may allow for considerable expansion of taxonomic representation in a collection, especially for nonmodel species. In addition, data collected from specimens of captive origin may be valuable to studies in which the taxon would otherwise be lacking (figure 5). Natural history museums would certainly benefit from the rich life history records that zoos focus on, because these data are largely unavailable to the museum community.

Current collaborative efforts. Existing collaborations between zoos and museums may illustrate shared opportunities and mutually beneficial relationships. In figures 1-4, we show several examples of existing collaborations between zoos and museums and demonstrate a range of benefits for these collaborations. Although zoos and museums occasionally exchange specimens, samples, or data, these exchanges are still relatively infrequent and represent a very small percentage of the collection holdings of either zoos or natural history museums. When exchanges do occur, they are typically the result of connections between individual museum staff (collection managers or curators) and zoo staff (curators or veterinarians), instead of a systemic and long-term collaboration that is established between the institutions. Although the AZA accreditation guidelines encourage specimens to be deposited in natural history museums postmortem (AZA 2021a), large-scale collaborations are typically not initiated by the leadership of zoos or museums or specifically by interinstitutional organizations (e.g., AZA, the Society for the Preservation of Natural History Collections, and other scientific societies). We recommend the staff at zoos and aquariums consider the long-term benefits of having a largely intact specimen (versus the destructive sampling of a full necropsy) for future study at a museum, when it is possible to do so. Even in cases in which the entire voucher specimen may not be available for depositing at museums, the tissue or DNA samples from these animals (along with the associated data) can continue to be a valuable resource (Buckner et al. 2021, Card et al. 2021, Thompson et al. 2021).

Challenges to collaboration and integration

Zoos and natural history museums have distinct cultures, values, organizational structures, research agendas, data management systems, professional societies, and funding strategies. In addition, there are logistical challenges of linking two different types of institutions. These differences can create barriers to effective communication and productive collaborations, but articulating the differences clearly

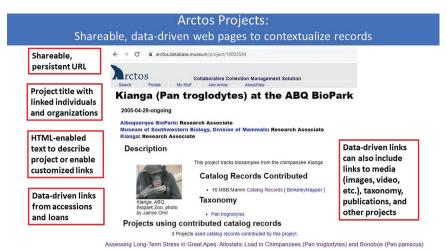


Figure 3. One example of a collections management system that can connect living and preserved specimen databases is the Arctos Collection Management system, a web-based multi-institutional collection management platform that currently handles thousands of records of specimens and biosamples from zoo-museum collaborations. Arctos museum records can be reciprocally linked to any external URL, creating the potential to form direct links with zoo databases such as ZIMS. Linking data between museum collection records and zoo databases will allow tracking of samples and their usage over the lifetime of individuals and beyond across multiple facilities and institutions. Data approved for public access can be searched through the main Arctos portal at https://arctos.database.museum and through biodiversity aggregators such as GBIF, enabling sample, project, and trait-based queries to extend the value of these samples and data for future research. Image: Mariel Campbell.

can help identify commonalities and focal points for collaboration. In the present article, we highlight some of the challenges to working across collection types, and identify actions to surmount these challenges.

Distinct institutional cultures and values. The underlying cultural differences between staff in zoos and natural history museums are multifaceted and complex, although they each hold at their core a passion and keen interest in biodiversity and the natural world. In the present article, we focus on several tangible and relevant elements of these differences such as different terminologies and attitudes toward specimens. Different terminologies used between institutions (box 1) can inhibit effective collaboration. Because of distinct and largely separate cultures, perceptions of one institution type by another may be outdated or erroneous. Making these misconceptions explicit and correcting them may help bridge cultures and find common institutional values and research objectives (see the "Different research priorities and agendas" section).

One major critical distinction between the values of zoos and museums is an affective attachment to living animals in zoos (Hosey and Melfi 2012), to which there is little to no apparent analog in museums. Through close daily interaction with individual living animals, long-term bonds between zoo staff and the animal they care for can be formed (Meehan et al. 2016). Such affection toward a specimen is rarely demonstrated for preserved museum specimens by museum staff. Comparatively, in museums, care for and attachment to specimens takes on several different forms: performing regular preventative conservation and maintenance; ensuring that specimens used for research are not damaged in such a way that could negatively affect their integrity; and ensuring that specimens are properly identified, and cataloged and that they have data that is made accessible to the public and researchers. In many cases, the history of the specimen tells a story that appeals to museum staff and may lead to some genuine attachment to the specimen and its story (such as who collected it, how long ago it was collected, whether it is a type specimen used to describe a new species, etc.). The sense that a specimen represents the past, but can be used into the future often leads to a great sense of responsibility among museum staff, who realize that their work today affects its usefulness in the future including in ways that are yet to be discovered or realized (NASEM 2020).

Different research priorities and agendas. The research priorities and agendas of zoos and museums vary, both in terms of their history and involvement in research and in terms of their research focus. Although both institutions may be involved in research, there is a longer history of scientific research and discovery within museums that may have aided in the development of more research-centric views in their institutional mission, whereas more emphasis is given to animal health and welfare within zoos. Museums typically list the contact information of curators and researchers openly on their websites, making research requests and collaboration relatively easy for users (e.g., other scientists interested in collections, members of the public). In comparison, the process of gaining access to information on zoo collections is less clear, and contact information is not readily available for most zoo collections.

In terms of research focus, collection-based research at natural history museums tends to have a wider focus, including basic biology (e.g., anatomy, biogeography, taxonomy, and systematics), evolution (Funk 2018), and more applied research (e.g., conservation and global change, Johnson et al. 2011, emerging infectious disease, Dunnum et al. 2017, Cook et al. 2020, Colella et al. 2021, Thompson et al. 2021). In contrast, several recent studies have reviewed research areas targeted by zoos, which illustrate most publications focus on applied research, such as animal sciences,

Overview Articles

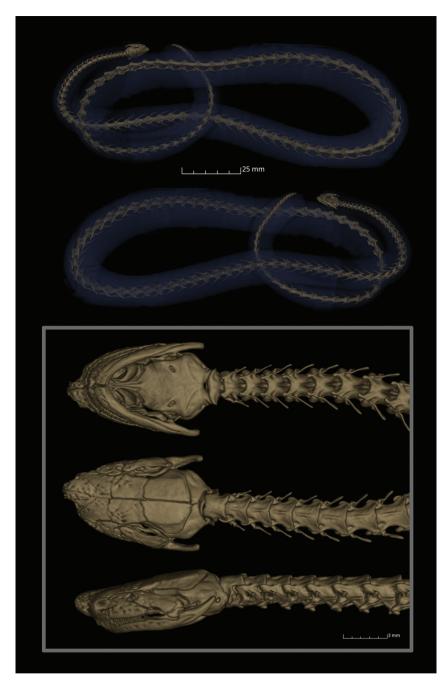


Figure 4. Since 2010, the Sedgwick County Zoo (SCZ) has partnered with the Yale Peabody Museum of Natural History to provide materials for use in a wide range of scientific studies including CT scanning, morphology studies and genome sequencing. SCZ has contributed over 770 specimens and samples to the Museum, including tissues and carcasses representing taxa from Gymnophiona to Proboscidea, and hopes to broaden communication with other potential partners to ensure maximum use of SCZ's resources. To date, specimens and tissue samples that the Zoo donated to the Museum have been used in more than 22 research projects and in university courses. Several SCZ specimens were scanned as part of the openVertebrate (oVert) Thematic Collections Network (NSF grant no. DBI-1701714), including YPM HERA 23166 (Potamotyphlus kaupii), which is one of two specimens of the species (each from SCZ) used to fill in a vital taxonomic gap in the oVert sampling. Scan data and reconstructions are now available via MorphoSource for use by researchers and educators globally (https://doi.org/10.17602/M2/M389815, https://doi.org/10.17602/M2/M389823). Image reconstruction: Jaimi A. Gray. The image is a rendering of a 3D reconstruction created from CT scan of specimen YPM HERA 23,166. CT scanning done at Nanoscale Research Facility at the University of Florida, with a GE phoenix v|tome|x m 240 micro-CT scanner, and was funded by oVert TCN (NSF grant no. DBI-1701714). Segmentation and rendering performed using VG Studio Max (version 3.5.1).



Figure 5. Patricia Brennan has worked with dozens of collaborators from farms to zoos to acquire specimens that died in captivity and whose bodies are ultimately preserved at museums for posterity, with Brennan facilitating that exchange after she completes her research. These include specimens of snake hemipenes (Nerodia rhombifer; M1) that are inflated with vaseline (M2) and then made into 3D models (M3). Specimens such as these require careful postmortem handling of animals, including rapid preservation. The connections and collaborations necessary to obtain such specimens have not been easy to establish, particularly as it is not always clear whom to contact for this kind of work at these facilities and this collaborative work is not usually part of the research mission of these facilities. Photograph: Bernard Brennan. 3D Images: Genesis Lara Granados and Juliet Greenwood.

behavior, cognition, husbandry, reproductive biology, welfare, veterinary care, or field conservation (Loh et al. 2018, Rose et al. 2019, Hvilsom et al. 2020). Museums also largely serve a research community outside of their walls, through specimen loans and, ever more frequently, digital data (e.g., CT scans online). Although zoo research also extends beyond the boundaries of the footprint of the institution, zoo collections are largely inaccessible to the broader research community.

Some museums may consider zoo specimens of low scientific value, because of the lack of locality data (i.e., the coordinates associated with the source population), possible effects of captivity on phenotypes (O'Regan and Kitchener 2005, Hartstone-Rose et al. 2014, Zack et al. 2021), potential adaptations to captivity (Williams and Hoffman 2009), hybridization of recognized or unrecognized taxa in breeding programs (Witzenberger and Hochkirch 2011), or necropsy practices. Although these issues may alter some aspects of the scientific value of specimens, there is considerable new research potential in using specimens from zoo collections to understand life history and demographics (Conde et al. 2019), to assess and predict the success of ex situ breeding and conservation translocation programs (Poo and Hinkson 2020, Poo et al. 2021), and for diverse downstream genetic and biochemical analyses (Witzenberger and Hochkirch 2011). In addition, the use of zoo specimens in systematics or anatomical studies, among others, is still of significant value, given the rarity of some taxa in the wild or the lack of availability of wild-origin specimens in museum collections. In other words, the benefits of using a zoo animal may outweigh the potential effects of captivity or the lack of locality data.

Another example of distinct research agendas (and agendas in potential conflict) involves destructive necropsies. When a zoo animal dies, there is a critical internal research need and institutional responsibility to conduct a detailed necropsy to determine a cause of death (Griner 1983, Terio et al. 2018). These necropsies are necessary in captive populations, because identifying the cause of death can lead to the prevention of similar issues arising in the remaining zoo population. In contrast, destructive necropsy can make some specimens less valuable to natural history museums, because it interferes with the study of morphology. However, for some taxa, a sample of tissue or blood alone may be invaluable to museums for future research, although it is important to consider that broad sampling of different tissue types may permit organ- or disease-specific sampling or unanticipated research by a broader range of interested parties. In addition to taking potential steps to reduce the destructiveness of necropsies for zoo specimens that are intended for museum transfer, improved communication and collaboration efforts on both sides would work to align research agendas to maximize the value of specimens to both zoos and museums.

Separate and nonoverlapping data management systems. The digitization and integration of biodiversity collection data have opened vast frontiers in scientific discovery (Conde et al. 2019, Nelson and Ellis 2019). Although both zoos and museums hold digitized data in sophisticated data management systems (Cohn 2006, Nelson and Ellis 2019), zoo and museum data are not currently integrated. Moreover, although both types of institutions purchase collections management software, those designed for natural history collection data are generally integrated with community science platforms that are publicly accessible through data aggregators, whereas those used in zoos are not accessible to the public or the larger scientific community through data aggregators or other means.

Box 1. Definitions to facilitate communication.

AZA. Association of Zoos and Aquariums, the primary organization that accredits zoos and distinguishes among modern zoos and roadside zoos or private animal collections. AZA requires high standards for animal care, recordkeeping, and engagement in scientific research.

Biobank. A repository for biological samples, typically for medical purposes.

Biocuration. Linking metadata about specimens so that information obtained from work with the specimens is retained or connected with the specimen's data in a digital framework.

Biofact. An artifact of organic origin (skull, fur, shell, horn, etc.), frequently used in zoos.

Cosmetic necropsy. Necropsy performed with minimal disruption to the body equal to a surgical incision. Often precludes full diagnostic value.

Conserve. Protect (something, especially an environmentally or culturally important place or thing) from harm or destruction.

Darwin Core. A body of data standards intended to facilitate the sharing of information about biological occurrences. Used by natural history museums, Darwin Core standards allow for data interoperability among software platforms.

Dynamic links. For example, a hyperlink between GenBank and a museum collection's database that would allow a user to find voucher information about the source of genetic data by clicking on a link. As opposed to static (unchanging) links that connect data repositories, which have a static catalog number that doesn't provide taxonomic or collection information and that cannot be automatically updated.

Extended specimen concept. A recent concept that a natural history specimen is more than a singular physical object, and instead that the specimen has extensions to potentially limitless additional physical preparations and digital resources.

iDigBio. Integrated Digitized Biocollections, the US National Resource and Coordinating Center for facilitating digitization and mobilization of information about vouchered natural history specimens. iDigBio aggregates specimen information from natural history collections across institutions.

MorphoSource. A digital repository of three-dimensional models of biological specimens.

Noninvasive research. Research that does not involve physical harm or distress to a living animal or specimen, i.e., photography or sound recording of living animals, CT scanning of preserved specimens.

Preserve. To safeguard and store the body, or parts of the body, of an organism, typically with a "preservative" such as ethanol and formalin or taxidermy, and associated data for future study.

Species360. A nonprofit NGO that produces ZIMS software, a database used by zoos to collect and store information on animals in zoo collections.

Specimen. A live or preserved organism (part of an organism) housed in a collection.

SPNHC. The Society for the Preservation of Natural History Collections.

SSP. Species Survival Plan Programs, AZA's programs to cooperatively manage ex situ populations for long-term sustainability.

TAG. Taxonomic Advisory Group, AZA's organized groups of taxonomic specialists who guide and facilitate cooperative animal management and conservation programs.

Voucher. A permanently preserved specimen deposited in an accessible collection.

ZIMS. Zoological Information Management Software, a software platform created by Species360 used by many zoos for collection and management of live animal collections.

Legal, political, and ethical barriers to collaboration. There are significant institutional barriers that can prevent effective collaboration. The ownership of individual animals in zoo collections is complex; individual animals may belong to the zoo where they live; may be on loan from another institution; or may be owned by state, federal, or foreign governments. A zoo that is holding an animal may require permission from the owning institution to provide samples to other institutions (even those collected noninvasively), and in some cases, the terms of a loan or holding rights may preclude the collection of samples from an animal or require the destruction of the specimen following its death. Although zoo animals that are of high scientific value may be worth these regulatory obstacles, advance planning may often be required long before the collection of samples from a zoo specimen or transfer of a deceased animal to a museum. Some foresight in negotiating these agreements may go a long way to negating these issues.

Hostility toward zoos by animal rights activists may also prevent sharing sensitive zoo data, including data related to primates, cetaceans, and elephants (Hosey et al. 2020) and other charismatic fauna. Some staff or administrators at zoos may feel that the nature—or the very existence—of their institutions and jobs are threatened by animal rights activists (Norton et al. 2012). Although the AZA has high standards of animal care that are continually raised and updated, there is concern that bad actors will seek to misrepresent any data and specimens that zoos make available. This alone may make many zoos reluctant to voluntarily share data on husbandry or medical records or even share samples or specimens from these sensitive groups.

Other regulatory barriers may exist in the forms of institutional animal care and use committee protocols, the Nagoya Protocol, and various permitting regulations including the US Department of Agriculture (USDA) Animal and Plant Health Inspection Service, the Endangered Species Act, the Convention on International Trade in Endangered Species, and the Migratory Bird Treaty Act, as well as biosafety and chemical safety regulations. The Nagoya Protocol itself may prevent the transfer of genetic resources (including samples or genetic data) without reference to the original permit or explicit permission from the country of origin. Even the physical process of transferring a sample will have regulatory concerns related to the International Air Transport Association, the USDA, or the US Department of Transportation, and possibly others. In general however, both zoos and museums are required to abide by many of the same laws and regulations, despite the change of some of these issues at the time of the animal's death. Navigating the regulatory labyrinth is key to successful collaboration. Although substantial obstacles may exist, given the degree of overlap in regulatory oversight, such navigation is not insurmountable. In fact, collaborating with museums with more experience with and infrastructure in shipping preserved specimens may benefit zoos; likewise, collaborating with zoos that have high standards of animal care and welfare could benefit museum staff that are collecting, handling, and euthanizing animals in the field.

Actions moving forward

Increasing the connection between zoos and museums requires concrete steps to be taken to link their digital data, transfer physical specimens across institutions, and create a shared, collaborative, research culture.

Data link and data accessibility. Both zoos and natural history museums have extensive databases critical to the holistic understanding of animal biodiversity (Suarez and Tsutsui 2004, Cohn 2006, Conde et al. 2019, Heberling 2020). Although the databases are currently not connected, the opportunity to link their data exists through the Darwin Core metadata standards (Wieczorek et al. 2012), which would permit greater integration of data. Although it may not be possible to fully integrate zoo and museum databases using existing infrastructure, integrating data under a common format is certainly an achievable goal in the near future. A shared data language standard will ultimately lead to connecting the information of living and preserved specimens.

Although zoos are understandably reluctant to make sensitive animal data public, the collection management software used by zoos could offer public access to limited data-at a minimum, as a list of species held by an institution or the number of individuals currently held for each species with their accession numbers. Given the public nature of many zoos, some of this information (e.g., the number of species and individuals) is already present for visitors to see and, therefore, sharing such information should not be controversial. Even this basic level of transparency would allow scientists anywhere with research needs to be able to find zoos that hold animal species they might find useful for noninvasive research projects. This level of accessibility would also allow natural history museums to search for individuals at zoos and make requests for tissues or to arrange for transfer of specimens to research collections at the end of an animal's life. We have found that one of the most common frustrations among zoo and museum researchers is not knowing whom to contact at the other institution type in order to begin a collaboration (figure 5). Having a website or accessible documentation listing the various roles and contact information for researchers would help facilitate valuable cross-institutional collaborations. We recommend that at least one email address (potentially anonymized for sensitivity) be a dedicated contact for research inquiries. Although it is possible that unwanted inquiries may occur when contact information is made public, the benefits likely outweigh the potential costs. We suggest, as a more localized first step, that zoo and museum staff in relatively close proximity reach out to one another to open lines of communication; we also suggest that interested zoo and museum researchers build coordination and collaboration networks to better address some of the issues raised in the present article.

Specimen and accompanying data transfer. Natural history museums have the capacity to preserve animal specimens, samples, and data in perpetuity. Many zoo animals have high scientific value as living or preserved specimens: rare or endangered animals that cannot be responsibly collected in the wild today, populations destined for reintroduction programs (especially those from which DNA or germlines can be stored for future use; e.g., in long-term longitudinal studies of population genetics), or individuals that have been intensely studied during their lives that can serve as important vouchers for future study. The transfer of specimens from zoos to museums can be divided into two categories: during an animal's lifespan (tissues, blood, DNA, gametes) and postmortem (skeleton, organ, whole specimen). In the former case, collections space within museums can provide a long-term repository permitting the use and study of these samples along with the many other "wild" collections made by these institutions from natural history fieldwork. In the latter case, transfer of animals to natural history museums postmortem would allow research in these individuals to continue for decades or centuries, including research that

could help protect and restore biodiversity in the future. To minimize physical damage to zoo animals during postmortem examinations, "cosmetic" necropsies can be performed to preserve the integrity of the scientific specimen. Although less destructive pathology techniques would be valuable, museums are also accustomed to finding great value in some field-collected specimens in less than pristine condition, including highly degraded road kills or specimens freed from the stomach contents of other preserved specimens (Hoving et al. 2013, Hieb et al. 2014). When a zoo specimen is transferred to a natural history museum, both zoo and museum databases should cross-list unique identifiers (e.g., catalog or accession number), so that each institution can track transfer of the specimen. When possible, dynamic links that can allow information from both collection databases to be updated simultaneously should be used, these dynamic data links are for the benefit of both institution types and anyone searching for this information (figure 3).

Contributing to the extended specimen concept and greater accessibility. During the first two decades of the twenty-first cen-

tury, biological specimen collections held in museums and academic institutions have been heavily affected by technological and collections-based innovations. The advent and rapid rise of digitization, for example, has resulted in huge numbers of digital replicas (e.g., CT scans, photographs) of physical specimens being made accessible online. This has led museum curators and collections managers to explore methods for linking their specimen records to related data within and outside of their institutions (e.g., related records from the same collecting event, GenBank records and other sources of genomic data, field notes recorded by collectors, and taxonomic treatments). The publication of The Extended Specimen (Webster 2017), follow-up work by the Biodiversity Collections Network (Lendemer et al. 2020), a National Academies biological collections report (NASEM 2020), and the Alliance for Global Biodiversity Knowledge Discourse consultation facilitated by GBIF (phase 1, www. gbif.org/event/2rUVeHayibJnajGOYgimja/digital-extendedspecimen-first-phase-community-consultation, and phase 2, www.gbif.org/event/6FF3aaAHoIkD9JToJjN4Vw/digitalextended-specimen-2nd-phase-community-consultation) have secured this concept in the literature and launched efforts to more precisely circumscribe the concept of turning a physical specimen into a linked and digitally extended specimen that would have added value for enriching biodiversity research.

The integration of zoo and museum data collected from a single animal is a fitting paradigm for the digital extended specimen concept. The data collected on living animals in zoos (e.g., blood and tissue samples, dietary patterns, behavioral repertoire, disease and illness records) may be far richer and more complete than museum specimens normally provide, especially for animals sampled across a lifetime. Assuming that zoo animals are deposited as specimens in natural history museums on their death, coupling records at these different institutes with bidirectional digital links ensures availability of these data to a broad range of researchers. These shared data can then be added to data aggregators (e.g., iDigBio, GBIF) that make these linked records even more widely accessible and underscore their important role in subsequent scientific efforts (Buckner et al. 2021). Specimens, living or dead, that have their metadata in databases will allow for a digital record to exist between the original collectors, caretakers, and curators. Likewise, these databases, when they are public, allow for accessibility that is often a barrier to equity when they are kept completely private. Some sensitive information may be restricted, but the more metadata that are publicly available and accessible, the more equitably the data can be used.

Bridging cultures. Bridging institutional cultures and creating a shared vision of how collections of living and preserved animals can be better integrated are key to advance scientific discovery of biodiversity as a whole. As zoos continue to build up their capacity for research (see AZA 2021a), there is a clear desire within the research community of both zoos and museums to increase cross-institutional collaboration and exchange of ideas. Scientists from both institutions can make progress through collaborative workshops, shared training sessions, expanding the pipeline for students and younger researchers from diverse backgrounds to work in both settings and for grants to foster the establishment of cross-institutional networks. Ultimately, broad institutional support is needed for lasting change, but a good place to start is through invitations to give seminars, tours of the different facilities, and other exchanges that foster sharing ideas and research by both institution types. It is important to recognize that although there may be cultural differences between institutions, many zoos and museums share the same ultimate goal of conserving species in the wild for the future. Recognizing the idea of an extended specimen concept and acknowledging that the best way to honor an animal may be to preserve it for generations to come can help bridge the differing cultures of zoos and museums. Ultimately, the pathway to bridging cultures requires collaborative initiatives with representatives from both zoos and museums, the development of human connections, and mutual understanding and trust. Although such a pathway may not be easy to traverse, it holds transformative potential for institutions and their staff, for the collections in their care, and for their wild counterparts that both institutions seek to conserve in perpetuity.

Conclusions

Increased coordination between living collections of zoos and the traditional collections of natural history museums is a logical and mutually beneficial relationship. Although nascent collaborations exist that demonstrate the potential of coordination, we argue that the interactions among institutions are severely underdeveloped. We identified areas where the most immediate connections could realize nearterm goals, including specimen transfer postmortem, data transfer postmortem, and permanent preservation of zoo specimens and associated data in natural history museums. Furthermore, we point to where a transformational impact could be made with long-term investments in bridging gaps between institutions, such as integrating zoo data with other biodiversity databases and expanding access to and the use of zoo data for biodiversity conservation and global change research. Ultimately, it will have to be the people who work at these institutions who bring cultural change by sharing their scientific ideals and approaches while creating personal connections that lead to collaborations and progress toward shared goals.

Acknowledgments

The present article was born in digital captivity out of the workshop "Linking and Leveraging Biological Collections: Zoos and Natural History Museums" hosted by iDigBio, Memphis Zoo, Zoo Miami, Yale Peabody Museum of Natural History, and University of Notre Dame and funded by the US National Science Foundation (under grant no. DBI-1547229). The images were provided by Bernard Brennan, Mariel Campbell, Jennifer D'Agostino, Genesis Lara Granados, Jaimi A. Gray, and Juliet Greenwood. Sinlan Poo and Steven M. Whitfield contributed equally to this work.

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