



A perfect storm for mammalogy: declining sample availability in a period of rapid environmental degradation

JASON L. MALANEY^{*} AND JOSEPH A. COOK

Department of Biology and David Snyder Museum of Zoology, Austin Peay State University, Clarksville, TN 37044, USA (JLM) Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87110, USA (JAC)

* Correspondent: malaneyj@apsu.edu

Natural history collections have stimulated insights into systematics and evolution, but the extensive biodiversity sampling held in museums is increasingly employed to address other critical societal concerns, especially those related to changing environmental conditions on our planet. Due to large-scale digitization efforts in the last decade, specimen information can now be collated across natural history museums. Here, we leverage the availability of digital records of specimens in the United States that span the past ~135 years to explore the vitality of this resource. Using mammals as an example, we document a significant decline in recent specimen acquisition at a time of extreme environmental degradation and loss of mammalian populations. To stimulate rigorous assessments of the impacts of changing conditions and future-proof this basic infrastructure for mammalogy, we recommend a renewed effort to build temporally deep, geographically extensive, and site-intensive collections of holistic specimens. Targeted fieldwork should be designed to leverage historic sampling to enable retrospective environmental analyses and derive more complete perspectives of change.

Key words: biodiversity informatics, climate change, monitor, natural history museum, specimen, voucher

An incomplete understanding of biodiversity on our planet compromises our ability to address complex societal problems related to food security, public health, biodiversity loss, and land-use changes (Barnosky et al. 2012). Identifying taxonomic boundaries is fundamental to many aspects of biology (e.g., conservation-Malaney and Cook 2013), yet even in wellstudied taxa such as mammals and birds, the rate of discovery of new species has increased in recent decades (Barrowclough et al. 2016; Burgin et al. 2018). One of the key resources for biodiversity discovery and mammalian systematics has been specimens and associated data archived in natural history collections. Conservation efforts also have relied on specimen data to document loss or imperilment of populations and species. Specimens grow in value over time because they often enable new insights not initially envisioned by the original sampling efforts. For example, availability of historical biodiversity samples from the Sierra Nevada by Joseph Grinnell and colleagues was critical to investigations of how environmental change over the last century has influenced morphology and genetic variation, and ultimately reshaped vertebrate communities (Moritz et al. 2008; Santos et al. 2017). New perspectives on biotic change (e.g., Hart et al. 2014) would otherwise have remained

elusive without the baseline environmental conditions recorded in natural history specimens.

In recent decades, however, the role of natural history collections has expanded to address questions in other disciplines (e.g., ecology, developmental biology, pathogen biology, physiology) due to development and deployment of new technologies that enable scientists to obtain detailed, comprehensive views of the biology of organisms (e.g., Pääbo et al. 2004; Willerslev and Cooper 2005; Soubrier et al. 2016). Here, we explore trends in specimen acquisition across time, space, and taxonomic diversity in mammalian collections of the United States. Digitization and online aggregation of data from vertebrate collections (Guralnick et al. 2009; Constable et al. 2010) have produced an accessible digital resource that allows summary views of critical research infrastructure. By using a relatively well-studied taxonomic group (mammals) and presumably well-sampled region of our planet (United States), we begin to assess the fitness of museum collections for current and future research demands.

Because collections have the potential to provide the key samples needed to investigate complex issues, we ask a pair of broad questions. First, are we building, maintaining, and

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making available the existing infrastructure at a level that ensures the sustainability of museums? Second, should we consider altering the way we build this resource so that it will meet challenges in the future?

MATERIALS AND METHODS

To quantify spatiotemporal collecting trends across the United States, we queried and downloaded all available mammalian specimen records from VertNet (May 2017, http://vertnet. org/-Constable et al. 2010; Guralnick and Constable 2010) from all 50 states (excluding Puerto Rico, District of Columbia, and other territories). These records are drawn from 68 museums housing mammals from the United States (Supplementary Data SD1; Hafner et al. 1997), including records from 18 of the 20 largest collections (Cook and Light, in press). We refined the dataset by removing records: 1) without date of collection, 2) without species-level taxonomic identification, 3) represented solely by photographs or audio, 4) donated from captive or domesticated conditions (e.g., zoos), and 5) of all fossils. We assumed that most natural history collections catalog, digitize, and publish new data within 2 years of the collection event. Consequently, we ignored data after 2015.

To examine variation in collecting through time, we tallied specimens obtained each year (1880–2015) using the "year" field reported by VertNet and calculated a 10-year moving average and *SD*, centered on each year. Then, to better understand long-term trends, we derived a quadratic polynomial regression from the 10-year moving average (with the most recent years, 2011–2015 excluded). We opted to use polynomial regression because preliminary analyses indicated that these museumbased data fail to conform to assumptions of other forms of regression. Because yearly fluctuations can be misleading, even when normalized across cohorts of years, we calculated decadal trends to more completely explore temporal tendencies in specimen acquisition.

For spatial analyses, we ignored specimens that lacked georeferenced coordinates but included all georeferenced records regardless of estimated spatial uncertainty. We examined spatial sampling at 2 scales. First, we tallied the total number of georeferenced records within each state. States are the geographic level of permitting and regulation, so comparisons at this scale provide some insight into past levels of sampling despite the unequal sizes of states. To gain an improved understanding of disparity across states, we corrected the number of specimens collected in each state by differences in land area using log-log regression of the number of specimens while accounting for areal size of each state. Below the state level, we ignored counties because some states lack these designations (e.g., Alaska), counties vary considerably in size (range: 34 km² for Kalawao County, Hawaii to 52,071 km² for San Bernardino County, California), and many counties remain poorly sampled (e.g., some counties have no digitized mammal records). Instead, for our 2nd set of spatial analyses, we tallied georeferenced specimens within equally spaced hexagonal quadrats (10,000 km²) disregarding state boundaries. We then depicted sample density within quadrats across 10 bins using an exponential approximation ranging from low (0–10 specimens of any species) to high (> 2,500 specimens) to explore how spatial coverage varies temporally and to identify sites that were more consistently sampled (e.g., targeted resurvey efforts). To explore spatiotemporal trends, we examined sample density across 5 quarter-century periods (1991–2015, 1966–1990, 1941–1965, 1916–1940, and before 1916).

To examine variation in taxonomic representation of mammals in the United States, we tallied specimens across taxonomic orders. Because rodents are the most frequently encountered taxon during sampling and are often a focus of specimen-based research, we examined sampling across rodent families more intensively. We suspected sampling has been uneven across taxonomic diversity, so we compared sampling effort for both orders and rodent families to expected values (i.e., if sampling was even across diversity) using a chi-squared goodness-of-fit test. We then applied a post hoc test to evaluate if sampling for an individual taxon was significantly different than expected using a *z*-criterion test while applying a Bonferroni correction.

To drill down further into these data, 5 groups of mammals were selected to demonstrate a few of the broader historic trends in sampling and show opportunities for future collection development. We identified spatiotemporal variation in sample availability and provided greater detail on taxon-specific sampling across time and space. We purposefully focused on exemplar taxa across a spectrum of diversity including 2 species, 2 genera, and an order of mammals.

We used analysis of variance (ANOVA) to compare sampling effort both for all mammalian specimens in the United States and for targeted exemplar taxa sampled across decades by considering decades as independent sampling periods. We used a Wilcoxon test to evaluate whether decadal means were statistically different from the overall mean (samples per year average 1875-2015). To evaluate differences among decades, we used Tukey's honest significance difference (HSD) test. Because comparisons among individual decades may fail to completely capture temporal trends, we also conducted a temporal trend analysis. These data are not ideally suited to linear models, although minor violations are likely acceptable (Shahbaba 2012), so we applied a nonlinear filtering procedure for all temporal analyses that decomposes a time series into seasonal, trend, and irregular components using loess (stl routine, stats package, R version 3.3.1-R Core Team 2016). We set the smoothing parameter (s.window = "periodic," robust = TRUE) to optimize seasonal components identified by the loess smoothing procedure and retained default parameters set according to Cleveland et al. (1990) for identifying the trend. To evaluate significant, abrupt changes within the trend, we used *bfast* routine (bfast package version 1.5.7—Verbesselt et al. 2015).

RESULTS

We downloaded 2,271,816 specimen records of mammals in the United States from VertNet. About 30% of these were culled by our screening protocol, including many photographs and fossils. We detected 1,593,065 specimens that reported the state, and of those, 1,490,267 reported a specific year of collection. Finally, 1,050,732 specimens could be tied to a georeferenced locality. These data revealed that on average 10,951 (SD = 6,186; 1875–2015) specimens were generated annually with a range between 125 (1882) and 28,779 (1994).

Across digitized museums, aggregate growth of mammal collections generally increased for nearly a century, but that overall upward trend began to slow in the 1970s and despite temporary bouts of high sampling effort (i.e., early 1990s and early 2000s), growth is now much lower (Fig. 1; Supplementary Data SD2). In the last decade (2006–2015), acquisition of new specimens declined significantly ($F_{13,126} = 40.55$, P < 0.001), approaching a century-level low. Between 2010 and 2015, approximately 5,500 new mammalian specimens were added annually across all the mammal collections we analyzed,

a number comparable to the average number of specimens obtained during the Great Depression of the early 20th century (Fig. 1A). Overall, recent sampling has fallen to an exceptionally low rate (Supplementary Data SD2) and represents a trend detectable over at least 4 decades (1976–2015; Fig. 1B).

Sampling is uneven across areal scales ranging from states (Fig. 2; Supplementary Data SD3) to local quadrats (Fig. 3). State-by-state comparisons, for example, detected poor representation of total mammalian specimens across states and more broadly in several regions (Fig. 2). Twenty-two states, many from the Midwest and Southeast, show low specimen acquisition with < 0.1 specimens/km². Moderate sampling characterizes 23 states, with ≥ 0.1 but ≤ 0.3 specimens/km². Five states (California, Connecticut, Washington, New Mexico, and Arizona) have at least 0.3 specimens/km², with California the only state with > 0.5 specimens/km². No state averages at least 1 specimen/km² of land area. After correcting for areal differences



Fig. 1.—Temporal trends of specimen acquisition for mammals in the United States. A) New collections of mammalian specimens in the United States have fluctuated over time but new samples during last 2 decades are approaching a low not witnessed in the last century. The black dotted line represents the yearly count of samples available on VertNet (May 2017), with gray lines representing a 10-year moving average and *SD*. The green line represents a quartic polynomial that optimally fits the moving average, truncated to 2010 to accommodate potential lags in cataloging. B) Percentage changes in trends of new specimens acquired per decade, scaled to the previous decade, indicate precipitous declines the last 4 decades (red) despite a century of consistent increases (blue) in acquisition of new specimens.



Fig. 2.—Unequal sampling across states for mammals of the United States acquired between 1875 and 2015. A) Specimens acquired per km² of land area for each state, and (B) corresponding location of each state. Only California (dark green) has > 0.5 specimens per km² and 44% of states (22/50) are arguably chronically under-sampled with < 1 specimen per 10 km² (orange and red). No state has at least 1 specimen/km² of land area.

(Supplementary Data SD3), 82% (41/50) of states are within 1 residual value of the log-log regression line. We considered the 9 states either above or below the log-log regression line by an order of magnitude (> 1 residual value) to have comparably high or low sampling, respectively. Five states (10%) are more than 1 residual value above, while 4 states (8%) fall more than 1 residual value below. The latter (Alabama, Delaware, Mississippi, and Missouri) reflect exceptionally low sampling.

Vast areas of the United States (i.e., Alaska, Southeast, Midwest, and upper Great Plains) have chronically low sampling (10,000 km² quadrats with < 10 specimens) but other areas (i.e., western coastal states and Southwest) have higher sampling (quadrats with > 2,500 specimens; Fig. 3). These later regions were more consistently sampled (Fig. 4F),

whereas other areas show spatiotemporal disparity in sampling (Figs. 4A–E). No quadrat has at least 1,000 specimens acquired across all quarter-century periods.

Across all collections nearly 70% of specimens are rodents (Fig. 5A), a significantly disproportionate representation (37.0% more than expected; Fig. 5C) in museum collections. Didelphimorphia, although represented by just 0.34% of specimens in collections, reflects higher than expected sampling. In contrast, all remaining orders of mammals in the United States have fewer than expected specimens (Fig. 5A). Cetacea, in particular, is represented by < 1% of specimens and has poor sample availability with respect to diversity (-90.3% deviance; Fig. 5B). Similarly, bats (-38.9% deviance) in the United States are underrepresented (Fig. 5).



Fig. 3.—Spatial variation of specimen acquisition for mammals of the United States between 1875 and 2015 per quadrat (10,000 km²). Total mammalian specimens (n = 1,050,732) have unequal regional distributions, with some areas poorly sampled (red) and other areas with > 2,500 specimens (dark green).

Among rodents, cricetids dominate sampling with > 62.2% of all mammal specimens (Fig. 5B). This significantly disproportionate representation is at least 73.0% (deviance) greater than expected based on diversity (Fig. 5D). Six families (Aplodontidae, Myocastoridae, Erethizontidae, Castoridae, Muridae, and Dipodidae), when combined, constitute ~3% of all sampling. Aplodontidae and Myocastoridae, both represented by a single species in the United States, have exceptionally low specimen availability (< -80.0% deviance). Similarly, 3 families (Geomyidae, Heteromyidae, and Sciuridae) comprise nearly 59% of diversity, but < 35% of sampling when correcting for species richness (Fig. 5). Sciurids, in particular, have exceptionally low sampling (-53.1% deviance; Fig. 5D).

Across taxa examined, temporal sampling has been sporadic (Fig. 6) and we found a decadal effect for each taxon (P < 0.1; Tukey's HSD). Decadal sampling means appear to have been maintained at or above the overall mean for 75–100 years for each taxon, but then declined significantly in the most recent decade (Supplementary Data SD4–8) for most mammalian taxa (except *Odocoileus*). Rather than presenting multiple decadal comparisons here, we compare just the decade with the greatest sampling with the most recent decade. We present all decadal comparisons, however, in supplementary materials (Supplementary Data SD4–8).

Jumping mice (genus *Zapus*) are small mammals widely distributed across North America from the East Coast to far western Alaska. They are represented by 16,598 specimens spanning the last ~135 years; however, in the comparison between 2006–2015 and 1966–1975, we detected significantly fewer (628 versus 1,838, P < 0.001) specimens obtained in the

former (i.e., most recent decade). American pika (Ochotona *princeps*), a species generally associated with high-elevation habitats, has been infrequently sampled, with 10,758 specimens acquired over 135 years (~123 specimens annually). We found that significantly fewer (4 versus 172 annually, P < 0.001) specimens were obtained in the interval 2006–2015 when compared to 1986–1995. Deer (genus Odocoileus) are widespread in the United States and represented by 10,235 total records, but spatiotemporal sampling is uneven. The period 2006-2015 experienced a jump in the decadal average number of specimens (1,846 samples) largely due to a single archival event of > 1,700 tissue specimens in 2013 by a state game agency. Two other decades have a statistically comparable number of samples (1976–1985: 2,107, P = 0.57and 1986–1995: 1,381, P = 0.15). The ubiquitous and abundant deer mouse (Peromyscus maniculatus) shows the greatest overall representation in this dataset, comprising nearly 20% of cricetid and 14% of rodent samples (156,199 specimens). However, significantly fewer specimens (P < 0.001)were obtained in the last decade (6,232 specimens) compared to 1936-1945 (23,212 specimens). In contrast with that single species, across all bats (order Chiroptera) in the United States, we found a total of 99,384 specimens representing 49 species. We detected significantly (P < 0.001) fewer specimens obtained in the last decade (3,582) across all bat species when compared to 1966-1975 (18,982). The numerically dominant year of sampling differed for each taxon (Supplementary Data SD4-8) including Zapus (1995, n = 459), O. princeps (1987, n = 1,044), Odocoileus (2013, n = 1,708), P. maniculatus (1939, n = 5,216), and Chiroptera (1970, n = 3,927).

Fig. 4.—Spatiotemporal trends in specimens of mammals of the United States. Maps are 25-year time periods in reverse chronological order: A) 1991–2015, B) 1966–1990, C) 1941–1965, D) 1916–1940, and E) before 1916. Areas are additively scaled ranging from low (0–10 specimens = red) to high (> 2,500 specimens = green, each quadrat = 10,000 km²). The final panel (F) is a mosaic of areas and periods depicting several areas (darkest green) that have been consistently targeted.

DISCUSSION

Natural history collections will undoubtedly continue to provide fundamental infrastructure for species discovery and systematics (Ceríaco et al. 2016; McLean et al. 2016; Burgin et al. 2018). Although mammals are arguably one of the best-studied taxonomic clades, new species are still regularly identified and delimited based on a combination of closer examination of existing material and new collections from poorly sampled regions (e.g., Hope et al. 2016; Malaney et al. 2017). In addition to biodiversity discovery, however, new uses of systematic collections by other fields have expanded rapidly (Bi et al. 2013; Holmes et al. 2016; Pauli et al. 2017). New uses place increased demand on these collections and re-emphasize the critical need to ensure that this library of mammalian diversity is temporally deep, spatially comprehensive, taxonomically diverse, and available to address future research questions. Traditional and nontraditional uses of specimens point to a need to re-examine how we jointly maintain and build this critical infrastructure if we hope to maximally stimulate biodiversity sciences in the future.

Based on data from VertNet, we detected uneven sampling intensity in museum collections of mammals in the United

States across time (Fig. 1; Supplementary Data SD2), space (Figs. 2 and 3; Supplementary Data SD3), and taxonomic diversity (Figs. 5 and 6; Supplementary Data SD4-8). While these data have some limitations, largely because some museum records remain undigitized (Cook and Light, in press) and at least a third (34%) of the records we found are not georeferenced. Nevertheless, patterns of uneven specimen preservation likely reflect variability in sampling effort by individual museum scientists and this variability may limit the utility of this infrastructure for certain subdisciplines of mammalogy. Significant reduction in specimen acquisition in the last few decades, in particular, will undoubtedly curtail the impact of museum collections on mammalogy at a time when contemporary rates of environmental disruption (e.g., habitat conversion or degradation) are causing significant loss of mammalian species and populations (Barnosky et al. 2012; Ceballos et al. 2015, 2017; Santos et al. 2017). This perfect storm, rapid environmental change and declining sample availability, calls attention to the urgency for a renewed effort to plan, build, and maintain basic sampling infrastructure for mammalogy in the future.





Fig. 5.—Specimen diversity across mammals of the United States between 1875 and 2015. Sampling across mammalian orders (A) and rodent families (C). Outer rings depict the percentage of the total specimens per order (n = 1,587,921) or family (n = 1,087,369), and the inner ring depicts the percent diversity (species per order or rodent family). Respective percentage values are depicted in the legends. Chi-squared goodness-of-fit tests reveal unequal sampling between 1875 and 2015 across mammalian orders (B) and rodent families (D) in the United States. Percentage deviation (diamonds) and standardized residual of the standard normal deviate, z (bars) indicate sampling above and below the expected null. Post hoc, Bonferroni corrected z-criterion tests indicate some residual values as significant (bold bars).

Why the decline in acquisition of new specimens?—Declining acquisition of new specimens is likely a consequence of multiple interrelated factors and so determining why acquisitions are in decline may be complex. We identify and briefly address 5 issues we suspect may limit development of this primary infrastructure: 1) the perception that removal of individuals through museum collecting significantly impacts the integrity of natural populations and communities, 2) the assumption that nonlethal and less invasive techniques capture data quality comparable to holistic specimens, 3) tighter regulatory and permitting restrictions, 4) insufficient investments in specimen-based fieldwork, and 5) missed opportunities for alternative specimen sources.

First, we fully recognize that some populations should not be lethally sampled (e.g., some small populations of federally listed species). The hypothesis that the removal of individuals for museum sampling has a substantive negative impact on most wild mammal populations has been seldom tested, however. Limited analyses of both short-term (Sullivan and Sullivan 2013; Sullivan et al. 2013) and long-term (Hope et al. 2018) data that allow comparisons between removal versus nonremoval (e.g., mark-recapture) studies of terrestrial small mammals do not support the often repeated negative perception of museum fieldwork. Additional studies should be encouraged, but the relatively low number of individuals typically removed from local populations by traditional museum sampling of mammals likely falls below thresholds for sustainable removal. We suggest that most mammalian populations are likely resilient to responsible levels of collecting, as observed in other vertebrates (Poe and Armijo 2014), contrary to the argument that specimen collecting generally contributes to extinction (Minteer et al. 2014).

Critics of collecting suggest that nonlethal, or less invasive, sampling techniques and new technologies (e.g., digital cameras and remote tracking devices) are viable alternatives to preserving whole specimens (Marshall and Evenhuis 2015; Pape 2016). Observational techniques alone, however, fail to capture the breadth of data (e.g., morphology, parasites), diverse perspectives (e.g., tissue-specific responses), and natural integration across diverse disciplines possible when compared to holistic specimens, which can provide a variety of samples to multiple, independent studies (i.e., skin and skeletal materials, multiple tissues, endo- and ectoparasites, microbiomes, etc.—Bi et al. 2013; Rocha et al. 2014; Holmes et al. 2016). Coupling observations with minimal sampling of biological tissues (e.g., blood, feces, hair) is a step in the right direction and usually is preferred for critically endangered species, but

Fig. 6.—Archived specimens across time in the United States (1875–2015) for select taxa. Each panel depicts the decadal sum of sampling (bars), the mean and *SD* of each decade (whiskers), and the mean (dashed line) of sampling across all years. In general, there is an effect of decade (ANOVA, $P \le 0.1$) for sampling. Panels include, A) jumping mice (genus *Zapus*), B) American pika (*Ochotona princeps*), C) deer (genus *Odocoileus*), D) deer mice (*Peromyscus maniculatus*), and E) bats (order Chiroptera).

samples of biological tissues from noninvasive studies are seldom permanently archived and available to the wider community. Museums should be encouraged to partner with long-term sampling efforts and accommodate materials when the associated data quality is high. Such sampling still falls short of the holistic sampling that will allow more complete characterization of the biology of individuals and variation within and among populations and species.

Parasites and microbiomes are inadequately sampled by noninvasive approaches. Because parasites and pathogens are

often major drivers of population dynamics (Hudson et al. 1998; Kutz et al. 2005; Lafferty et al. 2006), whole specimen preparations that preserve the entire complement of parasite fauna provide opportunities for powerful views of demography, ecology, and others aspects of the biology of hosts and their pathogens (Hoberg et al. 2009; Cook et al. 2016).

When museum specimens and associated data are fully published online (e.g., ARCTOS) and tied to other databases (e.g., GenBank, VetNet), they also help to foster replicable, extendable, and integrative science (Popper 1959; Baker 2016). We urge an extension of the voucher specimen concept to include holistic sampling (i.e., skin and skeletal materials, multiple tissues, endo- and ectoparasites, microbiomes, etc.) to stimulate integration across diverse studies that can scale from molecules to ecosystems. In short, a growing literature documents why observational, noninvasive techniques alone often fall short of providing the multidimensional integration or rigor necessary to yield critical insights into changing conditions (e.g., Clemann et al. 2014; Rocha et al. 2014; Ceríaco et al. 2016).

Multiple state and federal permitting agencies now effectively limit general museum collecting, highlighting how regulatory actions are partially responsible for the decline in acquisitions of new specimens. While strict limits on severely imperiled species are reasonable, efforts to curb the regular preservation of samples from a diverse set of nonprotected species (i.e., those without formal listing) will significantly impede future research and ultimately hinder management and conservation (e.g., Thomas et al. 2013; DiEuliis et al. 2016). Curiously, while most states in the United States regulate scientific collecting of rodents, most do not regulate nuisance kills, even including some imperiled rodents, by state residents (e.g., shooting prairie dogs, genus Cynomys-USFWS 2009, 2013). For comparison, billions of mammalian deaths are due annually to anthropogenic causes including hunting (at least 12 million wild mammals are harvested from 35 million annual licenses, tags, and permits-USFWS 2017), urbanwildlife conflicts (200,000-300,000 annual take of nuisance wild mammals-USDA 2016), and mortalities from wind turbines (at least 600,000 bats annually-Hayes 2013), vehicle collisions (> 3,000,000 mammals per year in the United States-Romin and Bissonette 1996; Seiler and Helldin 2006; Coffin 2007), roadside debris (e.g., bottles and cans, ~500,000 mammals annually-Hamed and Laughlin 2015), and domestic cats (between 6,300,000,000 and 22,300,000,000 mammals in the United States annually-Loss et al. 2013). Land conversion, for which no estimates are readily available, may be the largest driver of permanent population loss for mammals, however (Ceballos et al. 2017). Combined, those numbers dwarf the estimated number of mammal specimens permanently preserved in the United States annually (mean = 10.951/year for 1875–2015; < 0.000002% of the *lower* estimate for domestic cats alone). Yet specimens represent the only physical record of mammals available for a particular year. The relatively few specimens preserved annually, unlike the billons lost to science (and society), are key to understanding threats to natural and human-mediated population declines (Remsen 1995; Patterson



2002; Santos et al. 2017), not to mention human health and well-being (Yanagihara et al. 2014; Dunnum et al. 2017). Given the vastly disproportionate numbers for mammals killed annually by humans, resistance to building museum collections appears to be a misplaced and misinformed perception.

Declines in acquisition of new specimens are partially due to reduced investments in museum fieldwork and curation in recent decades. Many organism-based scientists and researchers depend on the research infrastructure held by museums (~25% of articles in the Journal of Mammalogy-McLean et al. 2016), which was developed through long-term investments by various institutions or by the efforts of private individuals spread over decades. Today, we take advantage of specimen archives preserved by prescient scientists of the past. What will we leave future scientists in terms of materials that document the epic changes now underway? The United States Biological Survey, initially created in 1885 (Schmidly et al. 2016), contributed many of the earliest specimens. Subsequently, taxpayer-sponsored programs built existing mammalian infrastructure (Fig. 1) that was funded through individual research projects, many of those funded by grants from agencies such as the National Science Foundation. More recently, large federally sponsored programs, such as the Long-term Ecological Research (LTER) and National Ecological Observatory Network (NEON-Springer et al. 2016) programs, could have stimulated museum archives, but they have mostly failed to prioritize long-term specimen infrastructure (Cook et al. 2016). Those programs instead generally emphasize long-term observational data for mammals (e.g., mark-recapture) to advance the understanding of ecological and evolutionary responses to pathogens, species invasions, changes in climate, and land use (Kao et al. 2012), but they could be viewed as missed opportunities to build permanent research infrastructure. Each of those large initiatives, as well as improved collaborations between museums and natural resource agencies (Cook et al. 2017), zoonotic pathogen screening operations, and others that are collecting organisms could serve to build the long-term sample archives held by museums (Yates et al. 2002; DiEuliis et al. 2016; Dunnum et al. 2017).

Spatial and taxonomic sampling disparity.—We detected several regions in the United States that have few representative specimens (Fig. 3). The Upper Great Plains, for example, remains poorly sampled, but mammals in that region could provide critical insights into dynamic range shifts and related responses to climate change because of the transition between grassland and forest mammalian biomes and associated suture zones that reflect lineage contact (Remington 1968; Swenson and Howard 2005). The southeastern region also remains poorly documented, as evidenced by new distributional records and populations (Czech et al. 2017), but is thought to harbor a high proportion of endemic species (Jenkins et al. 2015). Other poorly sampled regions (e.g., Alaska's Interior and North Slope) are remote and difficult to access, but poor historical sampling will limit deeper understanding of responses to climate disruption (Hewitt 2000; Hope et al. 2015). Each of these regions has high potential to provide insights into ecological

and evolutionary responses of mammals to climate change (Kutz et al. 2005; Tape et al. 2016).

In contrast, the Southwest and western coastal states are generally represented by higher sample density, but specimen representation has waned over the past quarter century (Fig. 4). Most intensive sampling in the Southwest occurred from 1940 to 1990 but has subsequently declined, similar to other regions of the United States (except the Midwest, South, and Alaska). Spatiotemporal sampling disparity indicates that only a few areas have been consistently sampled across time. We detected just 6 areas with at least 1,000 specimens of any mammal obtained across at least 4 quarter-century periods (darkest green, Fig. 4F) and several other areas that have been sampled (> 1,000 specimens) across at least 3 periods (lighter green regions). Areas associated with National Parks (e.g., Death Valley, Great Basin, Great Smokey Mountains, and Yellowstone) and other federally owned lands (e.g., Bureau of Land Management, National Forests, and military lands) have had greater sampling effort historically, but sampling appears to have diminished recently (Fig. 4).

Disparity of sampling across taxonomic diversity may be due to several interrelated issues. Exceptionally high sampling of rodents likely reflects their abundance and relative ease of capture, preparation, long-term storage, and permitting, especially the cricetids (Fig. 5). Similarly, greater sampling (although statistically nonsignificant) for Didelphimorphia is likely because only a single species (*Didelphis virginiana*) is represented and is often obtained by museums due to highway mortality. However, limited sampling for cetaceans is partially due to the logistical difficulty of obtaining specimen material. Significantly low availability of bat specimens is perhaps the result of specialized sampling techniques (i.e., netting), compounded more recently by collecting moratoria by permitting agencies for most species.

Drilling down into selected examples.—Jumping mice (Zapodinae; Zapus) have been at the center of politically charged conservation efforts along the Front Range of the Rocky Mountains in Colorado and elsewhere for the past 2 decades because of their close association with mesic, undisturbed sites (Frey and Malaney 2009; Schorr 2012). Despite estimates of loss of hundreds of millions of dollars in private development and the expenditure of millions of federal dollars devoted to conservation and monitoring of this polytypic group (Industrial Economics 2002, 2010; USFWS 2010), our understanding of fundamental taxonomic units of North American jumping mice remains unsettled due largely to inadequate availability of archival samples (Malaney et al. 2017). The number of new specimens of Zapus acquired during the last decade is lower than that in any other decade of the 20th century (Fig. 6; Supplementary Data SD4). Fieldwork to produce specimens and associated studies of geographic variation have been largely unfunded by management agencies, favoring instead nonlethal techniques, yet geographic variation and biogeographic history are critical to designing effective management programs and establishing conservation units (Malaney and Cook 2013; Moritz and Potter 2013). Minimal additions to the archival infrastructure of relatively few specimens annually from ongoing monitoring programs would help to unravel the environmental factors and pathogens potentially influencing the evolution and ecology of these species (Malaney et al. 2013, 2017).

Across western North America, the American pika (O. princeps) generally occupies high-elevation sites and hypothetically has been negatively impacted by climate disruption (Beever et al. 2003, 2010; Calkins et al. 2012), although the IUCN classifies this species as Least Concern (Smith and Beever 2016). Natural history specimens provide insight into historical distributions and biogeography (Hafner 1993; Hafner and Sullivan 1995), demography, genetic variation, parasitology (Galbreath et al. 2009; Hoberg et al. 2009; Galbreath and Hoberg 2012, 2015), and more recently, dietary plasticity (Varner and Dearing 2014). Yet, acquisition of new specimens has severely declined in recent decades (Fig. 6; Supplementary Data SD5). Of 8,075 museum records for O. princeps, an average of just 4 specimens per year were obtained in the last decade (2006-2015). Poor sample availability for recent years contrasts with availability of specimens archived during the previous 2 decades (881 between 1996 and 2005 and 1,720 between 1986 and 1995), leaving future investigators with relatively little material to assess pika biology during the warmest decade on record (Trenberth 2015). While we are not advocating intensive sampling of sensitive populations, we do recommend a vetted plan for increased sample preservation, including better coordination between resource managers and museums to ensure proper preservation and future availability of hair, fecal, or other sampling (e.g., removal of post-reproductive individuals) of purportedly declining populations. Such efforts should be combined with thoughtfully designed sampling of more robust populations to produce an improved archive for future investigations. Concerns over the impact of climate change on persistence of O. princeps will undoubtedly be plagued by limited insight into their biology, especially if new samples are not regularly archived.

Cervids remain a management focus due to overharvest, habitat loss, and emerging pathogens among other assaults. In North America at the turn of the 20th century, populations of deer (genus Odocoileus) were severely depleted due to overharvest and disease, but today these species sustain large annual harvests in nearly all states except Hawaii (WAFWA 2018). We identified a total of 10,235 deer specimens acquired over the last ~135 years (i.e., approximately 50 samples annually across the United States; Fig. 6; Supplementary Data SD6). Weak sample infrastructure limits our ability to understand the emergence of pathogens such as Chronic Wasting Disease that devastated deer populations and curtailed hunting opportunities in some areas (Miller and Williams 2003; Dorning et al. 2017). Still, the number of museum specimens is eclipsed by an average harvest of 6,300,000 deer annually since 2000 (Lovett 2017). Such high harvest levels reveal missed opportunities to expand collaborations between museums and state management agencies that handle many potential specimens annually (McLean et al. 2016). For example, in 2013, the North Carolina Wildlife Resources Commission archived nearly 1,700 tissues (North Carolina Museum of Natural Sciences) as part of a targeted effort to understand Chronic Wasting Disease (Fig. 6; Supplementary Data SD6). That 1-year effort resulted in the largest annual archival event for deer (> 15% of total deer samples).

The deer mouse (*P. maniculatus*) is among the most widely distributed and abundant wild rodents in North America, with a range extending from central Mexico to Alaska (Bedford and Hoekstra 2015). Deer mice thrive in both natural and anthropogenically altered environments (Linzey 1989; Leis et al. 2008) and are an important pathogenic reservoir (e.g., for Sin Nombre virus, Hantaviridae). Previously archived specimens of deer mice (Fig. 6; Supplementary Data SD7) were key to identifying unknown viruses and the ecological associations related to their periodic emergence as a public health threat (Yates et al. 2002; Dunnum et al. 2017). Intensive field work related to documenting the distribution of this pathogen funded through the late-1990s produced a valuable series of specimens of this rodent. However, acquisition of new specimens has plummeted recently with an average of 623 new specimens added annually across the United States since 2005 (Fig. 6; Supplementary Data SD7), which is a significantly lower rate than in the prior 8 decades. Lack of regularly archived material across space and time will compromise our ability to monitor disease dynamics or provide further insights for their control and prevention. Reinforcing this model are the recent discoveries based on museum specimens of not only many new rodent hosts of new hantaviruses (Dunnum et al. 2017), but also newly discovered hantaviruses hosted by shrews and moles (order Eulipotyphla) and bats (order Chiroptera-Yanagihara et al. 2014).

Bats are in decline globally due to a variety of threats (Arnett et al. 2008; Boyles et al. 2011). For example, Hayes (2013) estimated that between 600,000 and 900,000 bats die each year from wind turbines in North America. O'Shea et al. (2016) estimated that in recent years, a similar number have died annually from fungal infections (i.e., white nose syndrome). When combined, those annual numbers are 3 orders of magnitude higher than the average annual number of bat specimens preserved for scientific research in the United States (~736 specimens annually across all bats, or an average of about 15 specimens per species; Fig. 6; Supplementary Data SD8). Even during the peak year of 1970 when 3,927 bats were archived, that number was less than a fraction of a percent (0.0065%) of the lower estimate of anthropogenic losses. Despite programs designed to monitor these losses, few of them produce specimens that are permanently archived. There have been significant declines in new acquisitions of bat specimens for at least 4 decades. We document 9,075 bats preserved within the United States in last 2 decades, but of these, fewer than 3,600 were cataloged in the last decade (Fig. 6; Supplementary Data SD8). When combined, perspectives that suggest collecting bats should cease (John 2017; Russo et al. 2017), if implemented, will significantly challenge our collective ability to investigate many aspects of bat biology or mitigate bat loss. Because specimens are often used in multiple studies and likely will continue to be used in the future, they meet the reduce, refine, replace guidelines for ethical take (Sikes et al. 2016). Indeed, a well-represented biodiversity archive may obviate the need for so many, otherwise disconnected, field research projects on live mammals.

A proposed plan: investing in sample infrastructure.— Without a renewed financial and scientific investment, our ability to investigate the causes or impacts of changing environments on mammals will be severely compromised in the United States in the near future. We briefly point to 2 initiatives that could improve this specimen-based infrastructure by calling for a transition to holistic sampling and for the development of a coordinated plan, scaling from local to planetary sample preservation, that focuses on leveraging both discovery and retrospective sampling.

Holistic specimens (i.e., skin and skeletal materials, multiple tissues, endo- and ectoparasites, microbiomes, etc.) yield complex, interrelated perspectives by facilitating integration across disciplines such as anatomy, genetics, virology, bacteriology, behavior, physiology, and geospatial analyses. Holistic specimens, if archived as part of existing monitoring protocols, would provide the sampling necessary to enable diverse insights into responses to changing conditions and allow investigators to not only observe change, but also capture underlying causation. Many environmental monitoring campaigns are now based on noninvasive observations (e.g., camera traps, markrecapture, track plates) aimed at detection, capturing fluctuations in populations, or shifts in community composition. If regular holistic sampling was added to protocols, more substantive (replicable, extendable, and integrative) insights into essential drivers of change (e.g., genetic variability, disease and other pathogen profiles, microbiome or isotopic shifts, adaptation to local conditions) would be possible.

State and federal permitting offices have become more restrictive in issuing permits for scientific collection of mammals (McLean et al. 2016), often without clear or justifiable policy statements. For example, some state permitting agencies now are prohibiting broad collections of specimens thereby limiting research to specific areas, restricting collections to a few species with no conservation concerns, numerically capping individuals allowed for removal, forbidding all lethal traps, or constraining trapping duration or season. Simultaneously, some natural resource agencies remove hundreds of thousands of individual nuisance mammals with limited archival efforts. We encourage a vigorous national debate on the potential effects of such regulations and permitting on scientific infrastructure. This debate should aim to develop accepted standards and best practices for permits and protocols that will build deep archives of select wild mammals at accredited museums.

Museums provide critical material for current research efforts, but their greatest contributions to science and society, as predicted by Joseph Grinnell (1910), will come in the future. That prediction has been repeatedly demonstrated (e.g., Hickey and Anderson 1968; Yates et al. 2002; Moritz et al. 2008). As such, museums should be viewed not only as hypothesis-enabling infrastructure, but also as hypothesis-generating infrastructure. Most research programs and funding opportunities are designed to meet current issues, but they are effectively unable to address future challenges because they do not contribute to long-term infrastructure. In contrast, specimen value increases with time as each "sample" is repurposed to address emerging hypotheses (Dunnum and Cook 2012). Recent innovations (e.g., ancient DNA, genomic, isotopic, microCT scanning, and geographic information systems analyses) are now mining new perspectives from historic specimens that were not considered by the original field collectors (McLean et al. 2016). Consequently, sampling efforts should not cease, instead, spatially dense and temporally repetitive sampling should be a priority.

Holistic sampling, when combined with repeated spatiotemporal sampling, stimulates integrated analyses aimed at deciphering not only the timing and velocity of change, but also underlying processes. Repeated sampling of targeted areas, including the Great Basin Resurvey (Rowe et al. 2009; Kohli et al. 2018) and Grinnell Resurvey (Moritz et al. 2008; Santos et al. 2017), has enabled key insights in western North America. State and federal public lands managed by the Department of Interior (e.g., national parks and refuges) and Department of Agriculture (e.g., national forests) could provide logistical support for field sampling and offer excellent opportunities to build sampling infrastructure for future evidence-based management, but we must rethink how best to meet current and future biodiversity mandates. Early field sampling on these federal lands led to new understanding of the diversity and distributions of fauna (Hall 1981; Knox-Jones, Jr. et al. 1986; Schmidly et al. 2016). Resource agencies are mandated to maintain viable populations of wildlife, but often develop inadequate (i.e., solely observation-based) monitoring plans for understanding or mitigating changing conditions (Jenkins et al. 2015). Now is the time to leverage the distributed resources of state and federal resource agencies and build critical and comprehensive infrastructure for the future. Developing and implementing a set of recommended actions to build sampling infrastructure could guide collaborative efforts between agencies and scientists (e.g., Morrison et al. 2017) and help equip future scientists to tackle challenges on the horizon.

Extrinsic challenges to biodiversity decline include habitat conversion, invasive species, and climate change which can increase incidence of population extirpation, and in some cases, extinction (Barnosky et al. 2012; Ceballos et al. 2017). The role of intrinsic threats, such as pathogens, is less appreciated largely due to poor sample availability and an extremely limited number of expert parasitologists (Brooks and Hoberg 2007; Hoberg et al. 2015; DiEuliis et al. 2016). Because museums have a proven history of providing material for rigorous studies, now is the critical period for renewed effort to build holistic biodiversity archives. Although these analyses are cursory, they demonstrate significant erosion of primary infrastructure in recent years, a finding that demands attention. In summary, we call for a reinvigorated commitment to funding, curating, and investigating holistically sampled museum specimens as a foundation for integrated studies of the complex responses of mammals to unprecedented environmental change in the Anthropocene.

SUPPLEMENTARY DATA

Supplementary Data SD1.—North American Natural History Museums reporting mammalian specimens to VertNet May 2017. Dots represent geographic location of each museum scaled by total specimens reported or published (http://portal.vertnet.org/publishers—Hafner et al. 1997). Red indicates museums not published and green represents museums that report holdings to VertNet.

Supplementary Data SD2.—ANOVA and temporal trend analyses of United States sampling of mammals. We detected a significant effect of decade ($F_{13,126} = 40.55$, P < 0.001). Post hoc evaluations included a Wilcoxon test to evaluate whether decadal means (boxplots) were statistically different from the overall mean (dotted lines) (top left). Tukey's honest significance difference (HSD) test was used to evaluate differences among decades with colors scaled (bottom left). Number of asterisks indicate relative adjusted significance (significant codes: *** = 0.001, ** = 0.01, * = 0.05). Trend analysis includes the data, sinusoidal seasonal fluctuations, trend, and remainder of variation (top right) along with trend breakpoints (bottom right).

Supplementary Data SD3.—Corrected disparity of specimens collected across states. Top: log-linear regression of the number of specimens considering state area. Blue symbols represent states within 1 residual value of the regression (solid) with those having an order of magnitude greater or less (green and red) sampling than expected for their respective size. Bottom: states for each respective residual value.

Supplementary Data SD4.—ANOVA and temporal analyses of archived jumping mice (genus Zapus) across time in the United States (1875-2015). Panels include yearly variance of count plus 10-year moving average and SD of samples generated (top left). We detected a significant effect of decades $(F_{13,126} = 5.546, P < 0.001)$. ANOVA box plots and significance tests across decades (center left) and from the overall mean (bottom left). Post hoc evaluations included Tukey's honest significance difference (HSD) tests used to evaluate differences among decades (colored boxes) and a Wilcoxon test to evaluate whether decadal means (boxplots) were statistically different from the overall mean (dotted line, bottom left). Number of asterisks indicate relative adjusted significance (significant codes: *** = 0.001, ** = 0.01, * = 0.05). Trend analyses for each species includes the data, sinusoidal seasonal fluctuations, trend, and remainder of variation (top right) along with trend breakpoints analysis (bottom right).

Supplementary Data SD5.—ANOVA and temporal analyses of archived American pika (*Ochotona princeps*) across time in the United States (1875–2015). Panels include yearly variance of count plus 10-year moving average and *SD* of samples generated (top left). We detected a nonsignificant effect of decades ($F_{13,126} = 1.562$, P = 0.105). ANOVA box plots and significance tests across decades (center left) and from the overall mean (bottom left). Post hoc evaluations included Tukey's honest significance difference (HSD) tests used to evaluate differences among decades (colored boxes) and a Wilcoxon test to evaluate whether decadal means (boxplots) were statistically different from the overall mean (dotted line, bottom left). Number of asterisks indicate relative adjusted significance (significant codes: *** = 0.001, ** = 0.01, * = 0.05). Trend analyses for each species includes the data, sinusoidal seasonal fluctuations, trend, and remainder of variation (top right) along with trend breakpoints analysis (bottom right).

Supplementary Data SD6.—ANOVA and temporal analyses of archived deer (genus Odocoileus) across time in the United States (1875-2015). Panels include yearly variance of count plus 10-year moving average and SD of samples generated (top left). We detected a nonsignificant effect of decades $(F_{13,126} = 1.654, P = 0.0791)$. ANOVA box plots and significance tests across decades (center left) and from the overall mean (bottom left). Post hoc evaluations included Tukey's honest significance difference (HSD) tests used to evaluate differences among decades (colored boxes) and a Wilcoxon test to evaluate whether decadal means (boxplots) were statistically different from the overall mean (dotted line, bottom left). Number of asterisks indicate relative adjusted significance (significant codes: *** = 0.001, ** = 0.01, * = 0.05). Trend analyses for each species includes the data, sinusoidal seasonal fluctuations, trend, and remainder of variation (top right) along with trend breakpoints analysis (bottom right).

Supplementary Data SD7.—ANOVA and temporal analyses of archived deer mice (Peromyscus maniculatus) across time in the United States (1875-2015). Panels include yearly variance of count plus 10-year moving average and SD of samples generated (top left). We detected a significant effect of decades $(F_{13,126} = 11.867, P < 0.001)$. ANOVA box plots and significance tests across decades (center left) and from the overall mean (bottom left). Post hoc evaluations included Tukey's honest significance difference (HSD) tests used to evaluate differences among decades (colored boxes) and a Wilcoxon test to evaluate whether decadal means (boxplots) were statistically different from the overall mean (dotted line, bottom left). Number of asterisks indicate relative adjusted significance (significant codes: *** = 0.001, ** = 0.01, * = 0.05). Trend analyses for each species includes the data, sinusoidal seasonal fluctuations, trend, and remainder of variation (top right) along with trend breakpoints analysis (bottom right).

Supplementary Data SD8.—ANOVA and temporal analyses of archived bats (order Chiroptera) across time in the United States (1875-2015). Panels include yearly variance of count plus 10-year moving average and SD of samples generated (top left). We detected a significant effect of decades $(F_{13,126} = 20.698, P < 0.001)$. ANOVA box plots and significance tests across decades (center left) and from the overall mean (bottom left). Post hoc evaluations included Tukey's honest significance difference (HSD) tests used to evaluate differences among decades (colored boxes) and a Wilcoxon test to evaluate whether decadal means (boxplots) were statistically different from the overall mean (dotted line, bottom left). Number of asterisks indicate relative adjusted significance (significant codes: *** = 0.001, ** = 0.01, * = 0.05). Trend analyses for each species includes the data, sinusoidal seasonal fluctuations, trend, and remainder of variation (top right) along with trend breakpoints analysis (bottom right).

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