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PERSPECTIVE

The five million bird eggs in the world's museum collections are an invaluable and underused resource

Miguel Ângelo Marini,[1*] Linnea Hall,[2] John Bates,[3] Frank D. Steinheimer,[4] Robert McGowan,[5] Luis Fábio Silveira,[6] Darío A. Lijtmaer,[7] Pablo Luis Tubaro,[7] Sergio Córdoba-Córdoba,[8] Anita Gamauf,[9†] Harold F. Greeney,[10] Manuel Schweizer,[11] Pepijn Kamminga,[12] Alice Cibois,[13] Laurent Vallotton,[13] Douglas Russell,[14] Scott K. Robinson,[15] Paul R. Sweet,[16] Sylke Frahnert,[17] René Corado,[2] and Neander Marcel Heming[1,18]

[1] Departamento de Zoologia, Universidade de Brasília, Brasília, DF, Brazil
[2] Western Foundation of Vertebrate Zoology, Camarillo, California, USA
[3] Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, USA
[4] Natural Science Collections, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany
[5] Department of Natural Sciences, National Museums Scotland, Edinburgh, Scotland, United Kingdom
[6] Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil
[7] Museo Argentino de Ciencias Naturales, MACN - CONICET, Buenos Aires, Argentina
[8] Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Claustro de San Agustín, Villa de Leyva, Boyacá, Colombia
[9] Naturhistorisches Museum Wien, Wien, Austria
[10] Yanayacu Biological Station, Cosanga, Napo, Ecuador
[11] Naturhistorisches Museum, Bern, Switzerland
[12] Naturalis Biodiversity Center, Leiden, The Netherlands
[13] Muséum d'histoire naturelle de la Ville de Genève, Genève, Switzerland
[14] Natural History Museum, Department of Life Sciences, Tring, United Kingdom
[15] Florida Museum of Natural History, Gainesville, Florida, USA
[16] American Museum of Natural History, New York, New York, USA
[17] Museum für Naturkunde, Berlin, Germany
[18] Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, BA, Brazil
† This author is deceased.
* Corresponding author: marini@unb.br

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ABSTRACT
The ~1.97 million egg sets (~5 million eggs) housed in museums have not been used in proportion to their availability. We highlight the wide variety of scientific disciplines that have used egg collections and the geographic locations and sizes of these collections, to increase awareness of the importance of egg collections, improve their visibility to the scientific community, and suggest that they offer a wealth of data covering large spatial scales and long time series for broad investigations into avian biology. We provide a brief history of egg collections and an updated list of museums/institutions with egg collections worldwide. We also review the limitations, challenges, and management of egg collections, and summarize recent literature based on historical and recent museum egg materials.

Keywords: avian biology, collection-based science, egg collections, eggs, metadata, spatial scale, time series

Lay summary

- The 5 million bird eggs in museum collections are an invaluable and underused resource that could be used for a variety of studies.
- We describe briefly the history of eggs that were collected worldwide over the last 200 years.
- We show that eggs from collections can be used to study ecology, behavior, evolution, classification, and species conservation.
- Several of the 300 institutions with egg collections that we list are already making them digitally available and physically accessible to scientists and the general public.
- We hope with this commentary to increase awareness of the importance of egg collections and improve their visibility and support.

Los cinco millones de huevos de aves en las colecciones de museos del mundo son un recurso invaluable y subutilizado

RESUMEN

Los casi 1.97 millones de conjuntos de huevos (~5 millones de huevos) depositados en colecciones no han sido utilizados en proporción a su abundancia. En este trabajo, destacamos la subutilización de las colecciones de huevos a pesar de generar datos en amplias escalas espaciales y temporales, para incrementar la conciencia sobre la importancia de las colecciones de huevos, mejorar su visibilidad para la comunidad científica, y mostrar que las colecciones de huevos ofrecen una abundancia de datos a gran escala espacial y temporal para la investigación de la biología de las aves. Proporcionamos una breve historia de las colecciones de huevos y una lista actualizada de museos/instituciones con colecciones de huevos en todo el mundo. También discutimos las limitaciones, los desafíos y el manejo de este tipo de colecciones, y fornecemos un resumen da literatura que utiliza dados históricos y recientes de colecciones de huevos.

Palabras clave: biología de las aves, ciencia basada en colecciones, colecciones de huevos, escala espacial, escala temporal, huevos, metadata

INTRODUCTION

Scientific collections provide critical data about biodiversity, yet some types of specimens are overlooked by the scientific community. We present an overview of a specimen type that documents a critical part of the avian annual cycle: eggs. Egg collecting has a long history and peaked between the 1890s and 1930s (Figure 1, Supplemental Material S1). In this paper we conduct the first comprehensive review of egg collections worldwide, including small, formerly overlooked collections, and to our knowledge the first major review since the North American inventory by Kiff and Hough (1985). We located data for ~5 million bird eggs, or ~1.97 million egg sets, collected over the last 250 yr and housed in hundreds of museums (Supplemental Material Table S1). Although eggs are the second most numerous type of bird specimen in museums after skins (Roselaar 2003, eBEAC 2020), they have not recently been studied in proportion to their availability, as evidenced by a relatively low visitation rate by scientists at even the larger institutions over past decades (Supplemental Material Table S2). This lack of use contrasts with an overall increase in use of biological collections from 1980 to 2004 (Pyke and Ehrlich 2010). In some museums, the use of egg collections has decreased in recent decades, as seen in visitation rates at the large egg collection at National Museums Scotland (NMS, Edinburgh, Scotland) from 1980 to 2019 (Supplemental Material Figure S1). One reason suggested for the low use of egg collections is that egg structure and morphology are of limited use in higher-level systematics (Mikhailov 1997), but we discuss a multitude of studies, including systematics studies, that have been and can be conducted on these collections, some of which have gained recent widespread attention (Stoddard et al. 2017, Birkhead et al. 2019). In an era of large datasets and broad spatial modeling (Lister et al. 2011, Heming and Marini 2015), egg collections, which are arguably one of the largest and most readily available sources of long-term avian breeding information, offer an important and relevant source of data for analyses of long time series (Figure 1) and large spatial scales (Figure 2).

USE OF EGG COLLECTIONS FOR RESEARCH

Most historical research using egg collections was related to the description and study of the evolution of egg colors, patterns, and morphology. Starting in the late 1960s it was realized that eggs also can be reservoirs of critical information on avian breeding biology (Harrison and Holyoak 1970, McNair 1987, Green and Scharlemann 2003) and environmental impacts (Hickey and Anderson 1968). A much wider use of eggs in collections followed, resulting in studies of many diverse topics (see review in Supplemental Material Table S3).

Preserved avian eggshells should be viewed as "voucher" specimens (i.e. those that help substantiate research conclusions; Kageyama et al. 2007). Eggs are instantaneous, well-preserved snapshots of bird breeding, contain information about past environments, and hold unique biological information not available in skins, skeletons, blood,

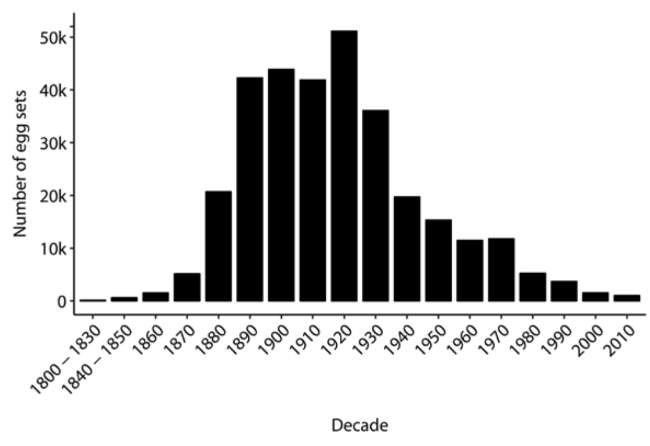

FIGURE 1. Distribution of 313,209 egg sets of birds collected by decade between 1800 and 2017, from selected collections available online or made available by curators/collection managers (WFVZ-USA, RMNH-The Netherlands, FMNH-USA, MNHG-Switzerland, AMNH-USA, NMBE-Switzerland, CAS-USA), and from 40 museums from South and North America and Europe with egg sets from the Neotropical region.

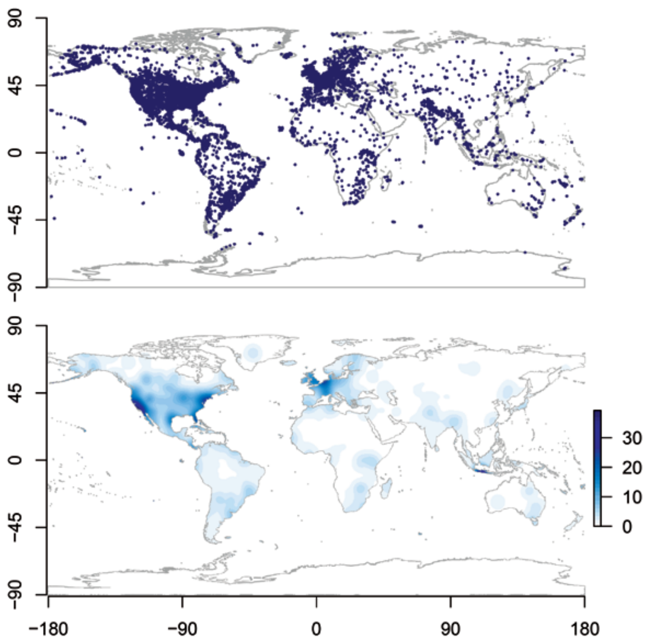

FIGURE 2. Global coverage of 269,783 egg sets of birds of the world collected since 1800 from selected collections available online or made available by curators/collection managers (WFVZ-USA, RMNH-The Netherlands, FMNH-USA, MNHG-Switzerland, AMNH-USA, NMBE-Switzerland, CAS-USA), and from 40 museums from South and North America and Europe with egg sets from the Neotropical region. Top = individual records; bottom = kernel-smoothed intensity function [e^1/2] from point pattern.

fluid-preserved specimens, tissues, or feathers. More recently, the usefulness of egg collections has increased with the availability of advanced analytical technologies, including scanning electron microscopy, spectrophotometry, several types of spectroscopy, chromatography, photogrammetry, genetic sequencing, and stable isotope analyses (reviewed by Burns et al. 2017). Digital photography (Bridge et al. 2007, Troscianko 2014) and noninvasive measuring tools such as 3D scanners allow for detailed measurements and modern image-processing. While data-rich specimens (i.e. specimens with associated egg slips with detailed data about the collecting event) are more valuable, even data-poor eggs can be useful for research requiring destructive analysis (Russell et al. 2010).

Eggs, because their dimensions do not change with time (Väisänen 1969), are well suited to studies of morphology. For example, a recent study of the eggs of ~1,400 bird species revealed that egg shape variation in birds is related to constraints induced by differences in flight (Stoddard et al. 2017). Olsen and Marples (1993) used differences in egg measurements of Australian raptors as evidence for subspeciation. Duursma et al. (2018) used egg collection measurements to show that passerine egg shape is influenced by climatic conditions such as temperature and humidity.

One of the main uses of bird eggs from museum collections is to study the evolution of egg colors and patterns. Changes in egg color patterns on egg surfaces have assisted in understanding the evolution of avian host/nest parasite relations (Spottiswoode 2010, Jaeckle et al. 2012). Eggshells could also assist with studies of sexual-signaling hypotheses (Hanley et al. 2010).

Eggs and eggshell traits are useful for phylogenetic and taxonomic studies (Sibley 1970, Sibley and Ahlquist 1972, Olsen and Marples 1993, Grellet-Tinner et al. 2012). Dried eggshells often hold material from the inner shell membranes, embryos, or shell powder that is useful for genetic analyses (Chilton and Sorenson 2007, Lee and Prŷs-Jones 2008). Further testing of historical museum eggshells for DNA fragments, as well as use of egg characteristics in phylogeny construction and resolution, could be a fruitful area of investigation.

Isotope analysis of eggshells of seabirds has expanded what we know about their foraging habits, geographic distribution, and differential use of marine and freshwater ecosystems (Schaffner and Swart 1991). Similarly, stable carbon and nitrogen isotopes of fossil ostrich eggshells were used to reconstruct Holocene paleoecological parameters in Egypt (Johnson et al. 1993), and the use of peptide markers to identify eggshells from a medieval archaeological site in the UK showed their potential to help understand historical egg use in human diets (Presslee et al. 2018).

Valuable natural history data for extinct, rare, and uncommon species can be obtained from egg collections (Maurer et al. 2010, Oskam et al. 2010). Egg sets can provide data about the historical demography of birds, including reproductive effort (based on egg sizes and clutch sizes), and breeding periods (Beissinger and Peery 2007, Blight 2011). New descriptions and updates on avian breeding strategies continue to be published, some of which have been based on formerly overlooked egg sets deposited in museums for nearly a century (McGowan and Massa 1990, Steinheimer 2004). Filling significant gaps in our knowledge has been slow for many groups such as Neotropical raptors (Monsalvo et al. 2018), and eggs in museums could be instrumental in assisting with additional information on historical distribution and breeding phenology of these birds.

Egg collections can provide historical information about early scientific exploration, and historical egg data can be used in association with data from nest collections (Ingels and Greeney 2011, Russell et al. 2013). Only 30% of the ~10,000 living bird species, mainly those from northern temperate regions, have well-understood breeding biology, with 39% moderately known and 31% still poorly known (Xiao et al. 2016). In our review of egg collections worldwide, we found broad geographical representation across regions in North America and Europe (Figure 2). Other geographical regions of the world, however, are largely undocumented, and thus represent fruitful areas for investigation. Filling these data gaps would increase opportunities to study regional differences in breeding biology (Green and Scharlemann 2003, Heming and Marini 2015).

The value of eggs to avian conservation is best represented by their role in long-term environmental biomonitoring, documenting the effects of chemical pollutants on eggshells (Hickey and Anderson 1968). During the period of heavy global DDT (dichlorodiphenyltrichloroethane) use from the late 1940s through the 1980s, hundreds of studies were conducted on eggshell thinning, egg content contamination, and embryo malformation (Hickey and Anderson 1968, Morrison and Kiff 1979). Egg sets from common species often consist of long temporal series (up to 200 yr) with broad geographic coverage, which can be used to study long-term changes in breeding traits, habitat loss, and climatic shifts (Scharlemann 2001, Green and Scharlemann 2003, Lister et al. 2011).

CHALLENGES, PREJUDICES, AND LIMITATIONS OF EGG COLLECTIONS

The majority of the world's egg collections have experienced curation challenges caused by funding, time, and staffing constraints (Dalton 2003). However, egg collections are, in some ways, easier to curate than skin collections because per specimen they need the same or less space; they are not as vulnerable to climate oscillations (especially humidity); and they need little or no protection against insect pests. Data from few egg collections are catalogued, digitized, and available online (but see CAS, FMNH, MVZ, NMBE, WFVZ, and YPM [institutional acronyms in Supplemental Material Table S1]). Furthermore, egg sets, like other bird specimens, are generally scattered among hundreds of institutions and countries. However, egg sets are concentrated in the 2 largest collections (NHMUK and WFVZ), which combined hold ~40% of the world's egg sets. This concentration is probably related to the lack of interest of many institutions in curating egg collections, and to donations to these 2 major institutions.

In the decades after the regulation of egg collecting began (i.e. approximately 1930s to the 1960s), a prejudice against historical egg collecting may have led to the relatively low use of egg collections by researchers (Birkhead 2016). However, once eggshell thinning due to DDT metabolites was shown to affect the breeding of many bird species, the stigma decreased, leading to a resurgence in use of museum eggshell materials. Despite this, some stigma remains attached to eggs collected by market collectors, as well as those that were sold and traded by private collectors (Barrow 2000). The nonscientific, amateur origin of many formerly private collections (Lightman 2000) can further stigmatize egg collections; as for collectors of study skins, some egg collectors have proven to be unreliable (Olson 2008). However, collections with problematic species identification can be overcome using modern methods of proving species identifications, such as genetic barcoding (Chilton and Sorenson 2007). General localities can be checked and improved with isotopic analyses (Hobson 2011). Egg sets have additional concerns that necessitate careful review of the specimens, such as the inability to determine or check species identification with skin vouchers, and uncertain clutch sizes (i.e. because the collector did not clearly state the size of the complete clutch), which can limit their scientific usefulness (Rasmussen and Prŷs-Jones 2003). In some collections, the disassociation between data (on original paper slips or egg cards) and egg sets can make eggs less readily useful than skins for research (Fisher and Warr 2003). However, digitization of field notes and original egg records, as well as sharing of provenance data among researchers and institutions, can facilitate realignment of records with egg sets.

Eggshells in collections may change color over time when compared with fresh eggs (Starling et al. 2006). Exposure to any light (not just UV light) can affect egg color. Furthermore, because their contents have been removed, historical egg sets cannot be used for proteomic analyses (Portugal et al. 2010), although proteins can be extracted from freshly collected eggs (e.g., Sibley 1970, Sibley and Ahlquist 1972) before they are made into eggshell specimens.

Fortunately, as for all museum specimens, researchers can overcome limitations by concentrating on reliable collectors who recorded relevant data, and by using large sample sizes of egg sets from several time periods, collectors, localities, and museums (Burns et al. 2017). While some biases have been reported in egg collections, such as higher proportion of larger clutches and early breeding dates, and a focus on mimics (Lack 1946; but see McNair 1987, Starling et al. 2006), such biases can be dealt with when recognized, as with almost any type of collection.

THE FUTURE OF EGG COLLECTIONS

The digitization revolution has greatly benefitted collections by improving data management, quality control, and data sharing (Peterson et al. 2005). For example, starting in 2005, the WFVZ partnered with museums in North America to put its egg and nest data online through ORNIS and other versions of NSF-funded public access portals (e.g., ORNIS2, VertNet, and iDigBio). As of 2018, data for more than 200,000 of the WFVZ's egg sets have been shared online, along with scans of original record cards and 83,000 photographs. Similar digitization projects have been implemented by other large egg collections (e.g., NHMUK and CAS).

Additional investments of time and resources can further improve egg collections. Data computerization, error checking, and taxonomic identification are needed, and in many cases, better housing of specimens will prevent damage over time (Stewart et al. 2015). Standardization of data (Aubrecht and Malicky 2010) can make egg sets more accessible to researchers. For example, databases should be compliant with Darwin Core Data Standards so that they can be shared online through existing data portals, and should include updated as well as historical taxonomy (Gill and Donsker 2018), specific collecting dates, specific locality data, georeferenced localities, and full names of the collectors. As with study skin data, use of egg set data is recommended only after validation of species identification and collection locality and date (Steinheimer 2010). The participation of all egg collections in the data-sharing community would make information more widely available for research and inter-museum collaborations (Peterson and Navarro-Sigüenza 2003, Peterson et al. 2005). Once digitized, these data should be made accessible via websites at individual institutions or through online portals such as the Arctos Collaborative Collection Management Solution (arctos.database.museum), the Global Biodiversity Information Facility (gbif.org), and VertNet (vertnet.org). Although this appeal for improved availability may seem obvious (Komen 1996), most egg collections are not yet available online, including none in Latin America.

CONCLUSIONS

Egg collections have been relatively underused, despite the investments in collecting and storing these eggs—with their data—through the centuries. Making egg collections more digitally and physically accessible will increase their use, and can inform the controlled, ethical, and planned collection of eggs that will be critical for many types of future science and monitoring (Winker et al. 2010, Joseph 2011). Likewise, nest collections and the deposit of non-specimen egg and nest data (i.e. photos with metadata) at museums can build up archived and accessible breeding information (Russell et al. 2013); hundreds of bird species still do not have a single clutch or nest represented in a collection. Furthermore, egg collections of some museums (e.g., FMNH, WFVZ, and YPM in the USA, and NHMUK and NMS in the UK) are still receiving historical egg collections from private collectors and small museums, and current specimens from researchers conducting field projects. A notable example is the effort by the ANWC, which has worked with Australian governmental authorities to legalize and transfer privately held egg collections to the museum (Joseph 2011). We hope that this commentary will increase awareness of the importance of egg collections and improve their visibility to the scientific community, leading to greater use of a relatively untapped resource documenting avian reproductive biology, life history strategies, and application to species conservation.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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Author contributions: M.Â.M. conceived the idea for the manuscript, and he and all other authors conducted the writing.

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