In April 2020, the Bronx Zoo made a headline-grabbing announcement: one of their tigers tested positive for COVID-19, a striking example of zoos as microcosms of human health and medicine. Indeed, many diseases and health problems experienced by zoo animals are found in, and frequently linked to, humans. Furthermore, the veterinary care they receive often incorporates knowledge, tools and treatments used in human health care. Here, we analyse these developments across the history of non-human primate health at the Smithsonian’s National Zoo and Conservation Biology Institute (NZP), one of the oldest zoos in the United States. From NZP’s opening in 1891, we distinguish five historical time periods within its first century based on how animal health was described, treated and understood. Concentrating on descriptions of primates in annual Smithsonian reports, we see notable changes in NZP activities focused on housing and environment (1889–1900), disease diagnosis and prevention (1901–1916), human–animal connections (1917–1940), research and collaboration (1941–1973) and conservation (1974–1989). We relate these shifts to concurrent medical events and trends in the United States, and interpret NZP’s history in a broader scientific and societal context leading to a ‘One Health’ approach to animal care and welfare today.

Keywords: zoo history, animal health, welfare, human medicine, primates

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INTRODUCTION

On 5 April 2020, the Bronx Zoo in New York City made a headline-grabbing announcement: one of their big cats, a Malaysian tiger named Nadia, had tested positive for COVID-19. At that time New York City was at the centre of the COVID-19 pandemic in the United States, with thousands of human infections reported daily. This was the world’s first known transmission of COVID-19 from a human to a non-human animal—most likely from an asymptomatic or pre-symptomatic zoo worker. Showing clinical signs of a dry cough and loss of appetite, Nadia underwent radiological analysis and blood testing before the Bronx Zoo decided to collect samples from her nose, throat and respiratory tract for COVID-19 testing. Two weeks later, it was announced that seven other big cats (four more tigers and three lions) had also tested positive for COVID-19, using a faecal sample test developed by the Bronx Zoo’s laboratory partners. All eight animals were reported as doing well following their diagnoses and were expected to fully recover.

This event is noteworthy for several reasons. First, the story increased public awareness that SARS-CoV-2, the virus that causes COVID-19, is zoonotic. Genetic evidence showed that bats were the likely wildlife origin, but scientists were only beginning to understand its potential to infect and sicken other species. Moreover, the event is an effective illustration of the zoo as a microcosm of human health and medicine. Indeed, many of the diseases and health problems experienced by zoo animals are found in, and frequently linked to, humans; COVID-19 is just one of them. In addition, this event demonstrated how the veterinary care received by zoo animals often incorporates—and frequently informs—knowledge, tools, and treatments used in human health care. As demonstrated by the innovative COVID-19 test developed for the tigers and lions, this work is constantly evolving in response to major events and new challenges.

The significance of the Bronx Zoo incident is borne out by historical zoo records. These records testify to the evolution of captive animal welfare and its intertwined relationship with human health and medicine since the nineteenth century. In this paper we report relevant health developments across the history of the Smithsonian’s National Zoological Park and Conservation Biology Institute (NZP), one of the oldest zoos in the United States and a unit of the Smithsonian Institution since 1890. Our main historical resource is a publicly available online archive of Annual reports of the Board of Regents of the Smithsonian Institution (hereafter Annual reports), which summarize the operations, expenditures and condition of all Smithsonian units for each fiscal year since 1847. These reports were submitted to Congress, which partially funds the Smithsonian through federal appropriations. As successive snapshots of institutional history, they provide an administrative framing of the major achievements and challenges of NZP from its

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beginning, with openness and emphasis on the most urgent financial needs of the time. From 1965, these *Annual reports* continue as the *Smithsonian year* series, but cease to provide detailed accounts of medical care and research at NZP after 1989.

Across the first 100 years of the zoo’s history, we distinguish five time periods based on how animal health was approached, treated and understood. We relate these historical shifts to concurrent medical events and trends in the United States, interpreting NZP’s history in a broader scientific and societal context, and in comparison with recent and ongoing NZP activities summarized in the penultimate section of this paper. Although NZP’s collection of animals has always consisted of a wide variety of species, we focus on non-human primates because of their vital role in many of the medical and scientific advances of the past century. The health-related information synthesized in this paper is especially beneficial to current and future research using non-human primate collections at the Smithsonian’s National Museum of Natural History (NMNH), which has acquired many remains of the zoo’s animals since the founding of NZP.

The thesis of this study is that NZP’s history is a mirror for the trajectory of human medicine in the United States—technologically as well as philosophically—owing to the growing awareness of interactions between animal and human health sciences over time. From the increasing use and integration of human health innovations in animal care, to the fuller recognition of human–animal health connections, to the prioritization of conservation medicine, we see the development of a holistic and interdisciplinary framework of ‘One Health’ (wherein human, animal and environmental health are interconnected) emerge through changes in activities, expenditures, staff and operations at the zoo. We also find visitors repeatedly reshaping the zoo-going experience, as enclosures were continually rebuilt and redesigned in order to meet the public’s sometimes conflicting preferences and expectations (such as naturalistic enclosures where you can always see the animals). This eventful and evolving path has led to NZP’s current approaches to animal care and welfare as a leading zoological park and research centre today.

### BEFORE 1889: SETTING THE STAGE FOR AMERICA’S NATIONAL ZOO

The late eighteenth and nineteenth centuries marked an important transformation from early animal menageries (e.g. the Ménagerie de Versailles and the Tower of London Menagerie) to the rise in zoological gardens throughout the world, including Europe (e.g. Schönbrunn Zoo in 1752, the Jardin des Plantes in 1793 and the London Zoo in 1828) and the United States (e.g. the Philadelphia Zoo in 1874 and the Bronx Zoo in 1899). In the United States, a new phase in the history of zoo design was slowly beginning by the 1880s, as critics of the bars and cages at American zoos began to call for more naturalistic enclosures. Not fully realized until after the opening of the Tierpark Hagenbeck in 1907, this approach began a transition in the treatment of animal collections from living cabinets of curiosities with a

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8 Hyson, op. cit. (note 6).
primary theme of taxonomic diversity to living museums in which animal habitats were of increasing interest.9

Although a few American institutions made an earlier transition from menagerie to proto-zoo centres for public recreation (e.g. Central Park Zoo in 1861 and the Lincoln Park Zoological Gardens in 1868), America’s first true zoo was the Philadelphia Zoo, which opened to the public in 1874.10 From its opening, it maintained detailed longevity records (births, deaths, acquisitions) for its collections and, beginning in 1901, any animal that died underwent a post-mortem examination.11 In New York City, the New York Zoological Park (now the Bronx Zoo) opened in 1899. With influence from the Boone and Crockett Club of New York, it distinguished itself from the menagerie style of the Central Park Zoo and communicated with the public about the park’s naturalistic qualities, including its relative seclusion and natural water supply.12 By 1902, the zoo aimed to establish a permanent medical department to ‘extend our knowledge of the care and health of wild animals in captivity, the causes of various diseases, and the means which should be taken for their prevention’.13 With the success of these institutions, a new standard for animal display and care had been established in the United States, both in public perception and, with increasing interest, by the medical community.

1889–1900: HOUSING AND ENVIRONMENT

The period of 1889–1900 is dominated by construction efforts, from the founding of NZP to the renovation and expansion of animal houses. The primary goal of NZP when it was established by Congress in 1889 (then named ‘the National Zoological Park’) was to preserve American species near to extinction.14 The American bison, for example, whose decimation in the late nineteenth century was documented by the first NZP director, William Hornaday, was a feature of its founding collection (figure 1).15 The plan was to seclude animals in large enclosures similar to their native habitats. There, endangered species would be protected and watched over by naturalists, with the hope that they could live and breed undisturbed.16 Most of the park was therefore intended to be a nature preserve, although a considerable portion of land was set aside for buildings, where animals of interest to the public would be taken ‘as expedient’.17 Under this plan, the main objectives of NZP were ‘useful and scientific’, with tourism being a secondary concern.18

17 Annual report 1891, op. cit. (note 14).
18 Ibid.
However, owing to limited financial support from the federal and city governments (which split the costs for the enterprise), NZP was replanned with a greater emphasis on recreation for the American taxpayers. Instead of large, open paddocks aimed at giving the animals as natural and undisturbed a habitat as possible, NZP’s collection would be housed and exhibited to the public in buildings.\(^9\) Frederick Law Olmsted, the father of American landscape architecture, whose work included Central Park in New York City and the grounds of the United States Capitol, designed the landscape and the location of the buildings in an area of Rock Creek Valley (now Rock Creek Park) in north-west Washington, DC. In 1891, given the pressing need and despite the lack of necessary funds, construction of a house for the animals began.\(^{20}\) Although NZP officially opened in 1891, the principal Animal House was not completed and fully occupied until 1893. Unfortunately, it was ‘merely a frame shed built in as cheap a manner as is consistent with safety and warmth’.\(^{21}\)

This early housing situation was a far cry from the original vision of NZP, but the *Annual reports* reaffirmed that the zoo did not have the money for more suitable accommodations

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\(^9\) *Annual report 1893*, op. cit. (note 16).

\(^{20}\) *Annual report 1891*, op. cit. (note 14).

\(^{21}\) *Annual report 1893*, op. cit. (note 16).
built of stone. Nearly all of the animals were kept together in the Animal House, so that the monkeys and tropical birds were confined with the big cats. The situation had not significantly improved by the end of the nineteenth century, as shown in figure 2, with animals from widely different regions crowded together in a single building with the same conditions of heating, lighting, ventilation and shelter. The small mammals were so inadequately housed that visitors complained. ‘Nothing can be done toward providing them with natural surroundings or with secluded breeding cages’, the Annual report stated in 1900. ‘In this the cardinal principle that was in view at the establishment of the park is violated, and something must be done to remedy these defects if any proper results are expected.’

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The animal collections at the zoo were diverse from the outset, as the empire of the United States expanded globally and NZP sought representative wildlife from the nation’s new colonial possessions.25 Indeed, the zoo would see its original mission fade during the early twentieth century, largely in response to popular demand for more exotic, entertaining and accessible animals.26 Animal health and well-being were a priority to the extent that these animals had monetary value as a tourist attraction while alive and active. Not until later in the twentieth century did zoo animals become seen by the general public as fellow creatures and—in the case of primates—close relatives, with rights to health and ecological value beyond scientific interests.

The care of the animals at NZP during this period was described only with respect to housing, evidencing how health perspectives and visitor expectations were managed. As many as 20% of NZP’s animals died in its first year, many immediately upon arrival because of injury caused when shipped or from being ‘too delicate’ to survive transportation.27 Even by this time, it was understood that animals coming from different habitats had highly variable needs, particularly with respect to temperature and protection, which were not being met. Careless feeding of the animals by the public was also a health threat: in 1895, a Diana monkey (native to West Africa) was poisoned after taking mountain laurel leaves from a visitor, despite efforts to keep this plant out of reach.28 The animal died in convulsions shortly thereafter, as reported in a local news story about the incident.29 By 1900, a house for small animals was made an ‘imperative’ priority and the principal Animal House was renovated, getting new flooring, a new boiler and a bigger heating plant to be able to properly maintain temperatures needed for the tropical animals to thrive.30

These first years of NZP’s history do not show a strong influence or involvement of medicine in the zoo’s basic operations, especially concerning the physical and mental well-being of the collection. The Annual reports did not specify any diseases among its animals during this period, and medical interpretations of animal illness were not provided. In contrast, by the 1890s, the zoos in London and Dublin already had a long tradition of engagement with surgeons and physicians, who learned about human health and human–animal relationships through interventions, dissections and experiments on zoo animals.31 These collaborations followed the emergence of veterinary medicine as a specialist branch of medicine in eighteenth-century Europe, with the founding of two veterinary medical schools in France in the 1760s.32 While NZP’s focus on the environment of its animals harks back to the sanitary movement of public health in the mid nineteenth century, which fixated on filth and ‘bad air’ as the cause and vehicle of disease, there was widespread acceptance of the germ theory of infectious disease in the United States by the end of the

26 Hyson, op. cit. (note 6).
27 Annual report 1891, op. cit. (note 14); Annual report 1893, op. cit. (note 16).
28 Annual report 1895, op. cit. (note 22).
30 Abigail Woods, Michael Bresalier, Angela Cassidy and Rachel Mason Dentinger (eds), Animals and the shaping of modern medicine: one health and its histories (Palgrave Macmillan, Cham, 2018).
31 Ibid.
nineteenth century. It thus seems most likely that concerns about poor housing were related to the safety, and perhaps financial, threats that they posed to the collection, rather than as conditions for contagion.

1901–1916: DISEASE DIAGNOSIS AND PREVENTION

The period of 1901–1916 reflects the growing attention to animal health at NZP. Housing remained a concern throughout this time, beginning with the first mention of poor mental health among the animals and ending with the building of NZP’s first hospital and laboratory. The behavioural and mental health impacts of the existing conditions, especially in social animals, were noted in 1901: ‘The higher apes and baboons rarely thrive in cages. Sooner or later they become abnormally vicious, or else have a complete physical breakdown.’ Following the reported deaths of 15 monkeys owing to ‘lack of proper housing’ in 1903, numerous additional structures were built. The construction of a new Mammal House for primates, rodents, small cats and armadillos began in 1905 and opened to the public in 1906 (figure 3). Adjoining the main Animal House, the Mammal House was notable for a glass roof that gave its occupants increased exposure to natural light. In 1913, an additional stone building that was ‘thoroughly sanitary’ had been constructed for preparing and storing food for the animals. Furthermore, an outdoor enclosure with a small shelter house was built specifically for monkeys in 1915.

However, this period is particularly significant for its focus on establishing a hospital, quarantine building and laboratory at NZP. The proposal to found a pathological laboratory to investigate animal diseases was first made in 1903 and was reiterated in Annual reports over the next decade. Without one, NZP partnered with the Pathological Division of the Bureau of Animal Industry (BAI), the federal veterinary service established within the United States Department of Agriculture in 1884. Under the auspices of this partnership, BAI pathologists performed most of NZP’s necropsies in the early twentieth century. Furthermore, in the absence of hospital and quarantine buildings, NZP’s sick animals were isolated ‘imperfectly’ with respect to their comfort and the prevention of disease transmission, kept in cages in the back of the stable away from the public. In 1913, NZP repeated its urgent need for these facilities to protect animal health, and to provide a place ‘where investigations of a zoological nature could be prosecuted for the increase of practical and scientific knowledge’. NZP’s first hospital, quarantine building and laboratory were eventually completed in 1916.

38 Annual report 1913, op. cit. (note 35).
The BAI lists the causes of deaths for many of NZP’s animals in their Annual reports of the Bureau of Animal Industry, beginning in 1903: for example, the deaths of one monkey from tuberculosis, one from a gastrointestinal condition and one from pneumonia. The diagnoses became more numerous and variable over the subsequent decades, including reports of osteomalacia, dysentery and other health problems during this period (see Electronic Supplementary Material). In the BAI report for 1911, it was stated that NZP’s animals frequently died of digestive or respiratory ailments, more than any other causes of death combined. While lack of sufficient exercise and unaccustomed climatic conditions were noted as important predisposing factors of these diseases, in numerous instances the microbial agents were identified. Tuberculosis continued to be ‘a menacing factor at the park’ and necropsies indicated that monkeys were especially susceptible to this disease.

The medical orientation of NZP during this period is striking in comparison to the previous years. By prioritizing on-site facilities for medical care and research, the zoo showed a desire

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41 Ibid.
to understand and learn from diseases in animals, contemporaneously with medical doctors. America’s first biomedical institute, the Rockefeller Institute for Medical Research (now the Rockefeller University), announced plans for a new animal hospital and laboratory to support animal experimentation by 1904. Infectious diseases in humans and animals were a dominant focus of medicine through the first half of the twentieth century, as increasing numbers of pathogenic microorganisms and their mechanisms of transmission were discovered. Serologic testing came into use in the 1910s as a basic tool to diagnose and control many of these diseases. Such medical advances are displayed in the specification and enumeration of causes of death among the animals at NZP, which are consistent with the deadliest human diseases at the turn of the century: pneumonia, tuberculosis, diarrhoea and enteritis were the top causes of human deaths in the United States in 1900.

It is unclear how much medical work was actually performed at NZP, as the zoo did not have its own laboratory facilities until 1916. Tuberculosis was a common concern at American zoos during this period, and local news stories described how the Bronx Zoo, Philadelphia Zoo and St Louis Zoo used quarantine and tuberculin testing in monkeys to prevent its spread among their collections.44 While it was reported that living animals at NZP were quarantined upon signs of illness, the extent to which diagnostic testing was used to confirm cases was not mentioned. Rather, disease diagnoses in the animals were determined through post-mortem examinations by the BAI, which used tuberculin testing for livestock surveillance and worked to eradicate bovine tuberculosis from Washington, DC as early as 1909.45 This BAI campaign followed a huge international congress on tuberculosis at the Smithsonian’s United States National Museum (now NMNH) in 1908, where the relationship between human and bovine tuberculosis was one of the big questions discussed.46

1917–1940: HUMAN–ANIMAL CONNECTIONS

The period of 1917–1940 shows an increasing concentration on medical knowledge and practice so as to enhance animal care, starting with detailed reporting of mortality data on the animals and ending with the zoo poised to hire its first veterinarian. The Annual reports from 1917 to 1929 included complete tallies of the causes of death among the zoo’s primates, but by 1930 NZP only necropsied animals if determining their cause of death might be ‘useful’.47 Keepers were vigilant about monitoring animals for signs of illness and isolated them in the veterinary hospital if necessary. When an animal died, its cause of death and necropsy report were entered into the final record.

Diet no doubt played a role in many of the causes of death reported for NZP primates during this period, such as digestive disorders like gastroenteritis, as well as metabolic...
bone diseases like rickets (see Electronic Supplementary Material). Zoo nutrition as a field of study was initiated in 1917 by Ellen Corsen-White, a pathologist at the University of Pennsylvania Medical School who investigated primate bone disease at the Philadelphia Zoological Garden.48 She eventually developed the recipe for ‘zoo cake’, a blend of grains, oil and chicken slurry intended to improve the nutrition of zoo animals fed commercially available produce.49 Although primates are generally omnivorous, NZP staff fed their monkeys and apes a primarily vegetarian diet consisting of boiled rice, bread, fruits and vegetables, and water.50 By the 1930s, as studies showed correlations between disease and nutritional deficiencies in protein, vitamins and essential minerals, researchers began recommending more regimented diets as the ‘key to disease prevention’.51 At NZP, these diets included supplementation ‘to balance their vitamins’ with cod liver oil, a known source of dietary vitamin D and treatment for rickets in human children during the early twentieth century.52

Notably, the influenza pandemic of 1918–1919 does not appear to have greatly affected NZP or its animals. Popular attractions like the Monkey House were closed briefly to prevent influenza from spreading through the weekend crowds in October 1918, as Washington, DC began implementing mitigation measures (e.g. school and business closures and cancellation of mass gatherings).53 These measures were taken to prevent human-to-human transmission of influenza, which was understood at that time as a crowd disease that spread between people via air and contaminated surfaces, although the infectious agent would not be discovered until more than a decade later.54 Nonetheless, the potential for zoo animals to be sickened by diseases from humans was already well known.

The intersection of human and animal medicine during this period, particularly with respect to zoonotic diseases, was discussed by the NZP director William Mann in his Wild animals in and out of the zoo (1930). His stories provide a wealth of information on the care and keeping of the zoo’s animals and provide insights into the thinking of zoo caretakers under his leadership (1925–1956). On the subject of zoonotic disease, he wrote about the importance of protecting apes from physical contact with visitors:

They must be kept as far from contact with human beings as possible, not only for the protection of the men and women but for the well-being of the apes. All these animals


are extremely liable to infections from humans, and when they are indoors, it is preferable to keep them in glass cages where the germs of respiratory diseases spread by coughing and spitting cannot reach them. An infection that would cause only a slight cold in a human being might cause fatal pneumonia or tuberculosis in an ape.\textsuperscript{55}

Mann also alluded to the physical presence of medical doctors at NZP in the 1930 Annual report, when describing the zoo’s many educational benefits: ‘The beginner in zoology gains at the zoo a grasp of the differences and likenesses between animals, while he rubs shoulders with the advanced medical man studying the primates to help him in solving problems concerned with the health of mankind.’\textsuperscript{56}

In the Annual report for 1932, there was a detailed description of an event that paralleled the Bronx Zoo cluster of COVID-19 cases in 2020. One of the great apes, a young gorilla named N’Gi, died after becoming ill with a bad cold, which progressed into pneumonia complicated with empyema. At the time N’Gi was sick, the chimpanzee in the adjoining cage also became ill and died. Both deaths were attributed to an outbreak of influenza in Washington, DC at that time.\textsuperscript{57} NZP called in a veterinarian to care for N’Gi, who received an X-ray examination and an oxygen chamber. When it was determined that a surgical operation was necessary, a local physician performed the procedure. Unfortunately, the long illness had so weakened N’Gi that he died shortly afterwards.\textsuperscript{58}

The cause of N’Gi’s initial illness from a human influenza virus is a reminder that NZP was (and remains) part of a large urban centre with continuous risks of zoonotic transmission. While pneumonia and enteric diseases remained significant health threats for the animals into the 1930s, Mann noted that tuberculosis became ‘actually very rare’ in the Monkey House.\textsuperscript{59} Here again the health of zoo animals and humans was shared: the tuberculosis mortality rate in the United States steadily declined from 1900 to 1940, becoming less than a quarter of the rate at the beginning of the twentieth century and dropping to the seventh leading cause of human death.\textsuperscript{60}

Medical care at NZP became more prominently reported during this period, as mortality statistics were replaced with descriptions of NZP’s efforts to treat sick animals, even if unsuccessfully. Human health experts were involved in some medical emergencies, and the latest medical tools were brought to bear on particular problems. In the case of N’Gi, for instance, radiology and oxygen therapy were available because of their increased human clinical use during the first half of the twentieth century.\textsuperscript{61} However, N’Gi’s high level of medical attention was most likely due to the fact that he was, as described by Mann, ‘easily the most important animal [NZP] ever had’.\textsuperscript{62} As the first gorilla at NZP in 1928, N’Gi was a huge public attraction at a time when very few zoos had gorillas. These rare

55 Mann, op. cit. (note 50), p. 85.
58 Ibid.
59 Mann, op. cit. (note 50), p. 94.
62 William M. Mann, Letter to Walter Chrysler, 7 December 1928, RU 74, box 75, Smithsonian Institution Archives.
animals were expensive and difficult to obtain and keep alive in captivity, often succumbing to the health impacts of infectious diseases, malnutrition, constrained environments and removal from their nurturing parents and communities at a young age. Among the urgent attempts to save his life, N’Gi’s X-rays were paid for by a local patron, who also arranged for the oxygen chamber and technicians that were flown into Washington, DC. The same oxygen chamber was used again for NZP’s only other gorilla, O’Kero, when he developed bronchial pneumonia shortly after N’Gi fell ill.

1941–1973: RESEARCH AND COLLABORATION

The period of 1941–1973 begins with the NZP’s investment in veterinary staff, and ends with major improvements in medical research capacity and technology. From 1941 to 1964, the Annual reports tracked the ascendance of medical research, scientific collaboration and evidence-based care for animals at NZP. In 1941, the zoo hired its first full-time veterinarian to provide ‘more careful dietary supervision, as well as much better medical and surgical attendance to the animals’. This hire was perhaps overdue, as veterinary medicine had been a formal discipline in the United States since the early 1800s and dozens of veterinary colleges had been established by the end of the nineteenth century. Moreover, the first zoo veterinarian was appointed to the London Zoo in 1829, and the first part-time zoo veterinarian worked at the Bronx Zoo in 1900. In 1956, another NZP veterinarian was appointed with three areas of responsibility: ‘to establish such a sound disease-preventive program through nutrition, sanitation, parasite control, laboratory examination, and environmental changes that the need for treatment and surgery is reduced to a minimum’; ‘to treat diseased and injured animals as necessary’; and ‘to carry on research looking toward better remedies and better health for the animals in captivity’. Assistance with post-mortem procedures and histopathologic examinations was provided by the National Institutes of Health and the Armed Forces Institute of Pathology, and a private physician, Joseph Watson, was named as consulting paediatrician for both the gorillas and the orangutans. The ‘Report of the veterinarian’ began to appear in the Annual reports in 1957, and a veterinary division was created shortly before the appointment of the veterinarian Clinton Gray in 1963.

The areas of responsibility listed above made it clear that science-driven activities and evidence-based decisions were expected in animal care at NZP. Seemingly all aspects of animal health were investigated rigorously by this period, producing an abundance of

64 Kara Arundel, Raising America’s zoo: how two gorillas helped transform the National Zoo (Mascot Books, Herndon, VA, 2017).
69 Ibid.
knowledge about causes and conditions of disease that were not understood in the preceding decades. In an appendix of the *Annual report* for 1941, the NZP assistant director, Ernest Walker, summarized the state of the science in his monograph *Care of captive animals*. He stressed that wild animals should be assumed to suffer from the same general types of ailments as humans and suggested that information gained from animal experiments to advance human medicine should also be used for the care of captive animals. In the *Annual report* for 1950, it was stated explicitly that ‘scientific research is not set up as a separate activity in the National Zoological Park but is an important part of the operation’ and that proper care for the animals called for constant observation and study of acceptable substitutes for their natural living conditions.

Although vitamin C was noted as ‘essential’ for primates in the *Annual report* for 1941, providing a healthy diet for the zoo’s animals was a challenge during World War II. Food rationing was implemented at many zoological parks including NZP, which had agreements with several stores and the US Marshal’s Office to collect vegetable trimmings, peanuts and soybeans judged unfit for human consumption. Primates were subjected to modified diets, with substitutions for their favourite foods, according to Mann, such as potatoes masked in honey in order to mimic bananas. The purchase of foods condemned for human consumption continued after wartime and contributed to keeping feeding costs down into the 1950s, even as specialized food mixtures with vitamin supplements were tested and used to feed at least some of the zoo’s primates and other animals.

Professional partnerships kept the veterinary medicine at NZP in lockstep with human medicine into the 1970s, helped by significant improvements in on-site facilities. Some detailed accounts of complex cases involved other veterinary laboratories and experts at times, as well as the continued treatment of the great apes by human doctors. For example, when a baby gorilla named Tomoka fell ill with an intestinal infection in 1962, local paediatricians were called upon for consultation. Tomoka did not respond to treatment and was taken to the Children’s National Hospital in Washington, DC, where he was placed in an animal research laboratory under the care of the resident physician. Diagnosed with shigellosis complicated by dehydration and acidosis, Tomoka recovered after this hospitalization. That same year, Tomoka’s father, Nikumba, received treatment from an orthopaedic surgeon and a neurosurgeon, after experiencing bilateral paralysis. By 1964, Nikumba had made a full recovery from a diagnosis of ‘selective spotty viral infection of the spinal cord’ following three months of drug therapy. The NZP veterinarian Clinton

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Gray published a detailed account of Nikumba’s illness, treatment and recovery the following year.\(^77\) In 1971 and 1973, Gray also published Tomoka’s treatment for rheumatoid type arthritis, a therapeutic regimen based on studies of rheumatoid disease in humans, in collaboration with the Arthritis Institute of the National Orthopedic and Rehabilitation Hospital in nearby Arlington, Virginia.\(^78\)

During this period NZP grew enormously as a research centre where animal and human health sciences intertwined. The zoo established an office (later department) of pathology with a primarily diagnostic function in 1968, organized a department of animal health, built a new hospital-research building in 1969, and expanded its surgery and radiology capabilities with major equipment purchases (including a portable X-ray and anaesthetic and electrocardiograph machines) in 1972. In *Smithsonian year 1973*, it was reported that NZP’s veterinary staff ‘has developed techniques and skill to permit difficult, complicated, and esoteric surgical procedures’.\(^79\) The work carried out by NZP and its medical partners represented some of the major scientific breakthroughs across the middle of the twentieth century, including the genetics revolution and the golden ages of antibiotic discovery and vaccine development that commenced in the 1950s. Furthermore, with the publication of *Veterinary medicine and human health* by the veterinary epidemiologist Calvin Schwabe in 1964, a holistic view of human–animal health connections began to bridge veterinary and human medicine and lead into the full emergence of One Health in the twenty-first century.\(^80\)

1974–1989: CONSERVATION

We identify a final period of significant change in the first century of NZP with its increasing focus on conservation science. This period begins with the founding of its conservation research centre and concludes with the end of the Smithsonian’s annual reporting on animal health and pathology. While conservation was the founding cause of NZP and has been central to its mission (efforts which continue to this day), the zoo reached a landmark event in 1974 with the establishment of its Conservation and Research Center (CRC). Fulfilling its long-held objective to establish a ranch-style ‘survival centre’ with more space for breeding groups of endangered species than an urban zoo could provide, NZP acquired vast space in Virginia’s Shenandoah Valley outside the town of Front Royal. Never open to the public, the CRC was created to support research and care that would help to save species from all over the world, with increased knowledge about animal biology, ecology and reproduction. Veterinary facilities at CRC were completed in 1985, providing the facility with a fully equipped animal hospital for surgery, hospitalization and clinical

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laboratory support for the animals there.\textsuperscript{81} In this work, across many decades, NZP moved from the traditional model of a zoo towards a world-leading centre for the captive breeding and reintroduction of threatened species.

The prioritization of naturalistic spaces also led to new enclosures at the zoo in the 1970s and 1980s, accelerating NZP’s change ‘from cages for containment of species to open arenas for awareness of the relationship of all living things’, as proclaimed in \textit{Smithsonian year 1974}.\textsuperscript{82} The zoo reimagined itself ‘from a consumer of animals out of the wild into a conservator and producer of animals and into a major zoological resource of animal knowledge that can be disseminated around the world’.\textsuperscript{83} For example, the remodelling of the 1904 Monkey House included structural features for swinging, climbing and leaping that reflected a better understanding of the habitual behaviours and health needs of its occupants. Likewise, the construction of the Great Ape House was completed in 1980, with grass-covered outside yards in addition to glass-fronted exhibit areas with artificial climbing ‘trees’ made of steel gunite. The description in \textit{Smithsonian year 1981} conveyed triumph: ‘It was thrilling to see mature gorillas and orangutans, who had never before had more than pipes and wooden shelves, climbing on their new trees.’\textsuperscript{84}

This style of zoo exhibits followed a transition towards ‘sanitary modernism’ that began in the 1950s and 1960s, with particular attention to questions of animal health concerning natural behaviour, rather than natural surroundings, followed by the subsequent development of landscape-immersion techniques during the ’70s and ’80s.\textsuperscript{85} Visitors became more concerned about the quality of life for zoo animals, as public awareness and activism in conservation grew.\textsuperscript{86} Further renovations of the Monkey House began in 1983, the same year that a new ‘Monkey Island’ habitat opened to the public (\textit{figure 4}).\textsuperscript{87} Consisting of a natural stone bluff bordered on three sides by water and landscaped with pine trees and aquatic plants, the island (now known as ‘Lemur Island’, with mixed lemur species) housed several species of animals including Barbary macaques, while illustrating for visitors the ecological and evolutionary relationships between animals and plants.

During this period, NZP’s Office of Animal Health and Pathology was heavily featured in annual reporting, both for new constructions and for research. By 1978, with a newly constructed necropsy building, autopsies were performed on every animal that died. Importantly, the building’s ample space and modern equipment facilitated detailed pathology work, including routine blood tests, urinalysis, cultures, parasite examinations

\begin{itemize}
\item \textsuperscript{83} \textit{Ibid.}
\item \textsuperscript{85} Hyson, \textit{op. cit.} (note 6).
\item \textsuperscript{86} David Hancocks, \textit{A different nature: the paradoxical world of zoos and their uncertain future} (University of California Press, Berkeley, 2001).
\end{itemize}
and a variety of other diagnostic tests. Also in 1978, the zoo hired its first official animal nutritionist. The following year, NZP’s hospital complex was expanded with a quarantine building, a nursery and an intensive care unit. The Department of Animal Health took a preventative approach in veterinary medicine, with yearly tuberculosis tests and physical examinations, as well as routine faecal examinations conducted on all primates. These data became more accessible for research and future use when NZP became the first zoo to computerize its medical records in 1982.

Due to NZP’s conservation focus, clinical medicine and reproductive physiology were strongly emphasized during this period. In 1983, the reproductive specialist David Wildt became an animal physiologist in the Department of Animal Health, which grew to include dozens of staff and collaborators. His work included reproductive research in endocrinology and the development of techniques in the areas of semen and embryo collection, transfer and cryopreservation in collaboration with the National Institutes of

89 Ibid.
Health, the National Cancer Institute and the Uniformed Services University for the Health Sciences.\textsuperscript{90} New procedures were formulated for long-term banking of spermatozoa and embryos, and considerable progress was made towards an embryo recovery and freezing programme for animals at the CRC.\textsuperscript{91} In 1987, NZP established an endocrine research laboratory in the veterinary hospital at the CRC, leading to the development of non-invasive techniques to determine ovulation, pregnancy and onset of labour.\textsuperscript{92} At the same time, NZP became the first research laboratory to produce carnivore offspring from \textit{in vitro} fertilized embryos, using a system developed by its own researchers.\textsuperscript{93} Further advances were made in gamete research, and embryo technology soon followed. By 1988, with the opening of a new veterinary hospital, clinical studies were underway to utilize and modify newer tools such as ultrasound, endoscopy and nuclear magnetic resonance.\textsuperscript{94} Other applied research included antibiotic testing for shigellosis, diagnostic testing for tuberculosis and prophylactic measures against viral hepatitis, diseases that threatened the primate collections.\textsuperscript{95}

Notably, this period parallels advances in human reproductive medicine in the 1970s and 1980s, with the first human born after conception by \textit{in vitro} fertilization in 1978.\textsuperscript{96} The sharing of knowledge across human and animal health was evident in direct collaborations, as well as in \textit{Smithsonian year} appendices that listed staff publications for each year. In 1984, NZP publications in \textit{Reproductive Biology}, the \textit{Journal of Andrology} and the \textit{Journal of Reproduction & Infertility} showed a broad dissemination of information about reproductive physiology and fertility from the Department of Animal Health. In these topics and many others, NZP’s researchers were directly and indirectly engaged in conversations with colleagues outside the zoo and across disciplinary divisions.

\section*{AFTER 1989: MODERN CHANGES IN ANIMAL CARE, WELFARE AND CONSERVATION SCIENCE}

When NZP celebrated its 100th birthday in 1989, its achievements in animal medicine were already considerable. The departments of animal health and pathology were not featured in the centennial issue of the \textit{Smithsonian year} series, and reports became extremely condensed starting in 1991. However, advances continued to be shared through research publications, popular articles, public outreach efforts and other products that provide the basis for a contemporary overview of NZP’s animal health activities in this section.
By the 1990s, NZP was well into the ‘era of the scientific curator’, where many animal management positions were held by PhD scientists. The culture of conducting science for science’s sake turned towards a strategic approach following NZP publications on the cost of animal inbreeding.\(^97\) The trend of conducting good-quality research to solve a problem was fully realized during this time. For example, to address the problem of golden lion tamarins nearing extinction in the wild, the NZP researcher Devra Kleiman spent over a decade building a reintroduction programme in collaboration with zoos around the world and local stakeholders in their native Brazil. By 2000, there was a thriving population of golden lion tamarins in Poço das Antas Biological Reserve and the surrounding area.\(^98\) Preparing these individuals for reintroduction relied on a strategic breeding plan and an intense programme to build physical strength and develop food resource strategies to increase the likelihood of survival.\(^99\) Although those born in zoos could not survive independently following reintroduction, their offspring were successful.\(^100\)

In addition to scientists and animal care experts, reintroducing individuals relied on health assessments to make informed decisions that would safeguard all involved.\(^101\) Prior to leaving NZP, a golden lion tamarin ready to be reintroduced was discovered to have antibodies for callitrichid hepatitis virus, a virus which is not present in their native habitat. NZP’s pathology programme and advanced diagnostic facilities discovered the antibodies that allowed staff to minimize risk in how reintroduced individuals were selected.\(^102\) The pathology team, under the leadership of Dick Montali, advanced veterinary diagnostics at a rapid pace during this time. They were the first to discover elephant endotheliotropic herpes virus, a lethal virus found in captive and wild populations, and helped to discover chytrid fungus, a lethal fungus decimating wild amphibian populations.\(^103\)

Along the lines of the innovative golden lion tamarin programme, animal management practices at NZP and around the world have increasingly focused on species-appropriate behaviour, enrichment, training and welfare. The concept of health expanded from physical needs to incorporate psychological needs as well, as reflected in many academic publications.\(^104\) Smithsonian Institution Press published many texts discussing these...
concepts and highlighting work by NZP staff as well.\textsuperscript{105} Incorporating these changes into animal enclosures meant that designs were planned by teams with experts from animal care, education and research, in addition to exhibits professionals. In 1995, NZP opened the Think Tank exhibit, a combination primate-housing and visitor education building that gave visitors a glimpse into how animals process information. For example, the staff emphasized the intelligence of orangutans with live research sessions in which orangutans could choose to participate.\textsuperscript{106} The ongoing exhibit includes another aspect of choice, an important feature of psychological well-being: the O-Line, a series of overhead cables that the orangutans can use to travel from Think Tank to the Great Ape House, locomoting high above the ground as they would in the wild.\textsuperscript{107} This feature helps provide opportunities for orangutans to individually decide where they want to be, and which group members they want to be with, much as a natural habitat would do.

Furthering NZP’s science-based mission, the CRC was renamed as the Smithsonian’s Conservation Biology Institute (SCBI) in 2010.\textsuperscript{108} By 2020, SCBI included more than 70 full-time scientists working in science centres and programmes dedicated to sustainability, genomics, ecology, species survival, migratory birds, working landscapes and global health. Combined with researchers working in veterinary medicine, nutrition and animal care, NZP became the most research-productive zoo in the Association of Zoos and Aquariums.\textsuperscript{109} For example, the NZP nutritional scientist Mike Power studies milk samples from primates to better understand their evolutionary past and to support offspring when mothers are unable to produce milk or care for their young.\textsuperscript{110} In line with modern animal management goals, participation from animals is voluntary. It is now widely understood that the ability to produce high-quality research and positive health outcomes depends not only on the ability of the scientists, but also on the training abilities and relationship-


building skills of zookeepers with their animals. One instance of this trust was displayed when a gorilla named Mandara, a seasoned participant in the milk study, allowed her zookeeper, Erin Stromberg, to collect a milk sample just three days after she gave birth to Kibibi.111

Through external partnerships and in training the next generation of scientists and practitioners in animal care and conservation biology, NZP is increasingly engaged with the medical community.112 As a partner in the Great Ape Heart Project, the zoo is among 70 institutions working together to address problems of cardiovascular disease in great apes, a professional community that includes veterinarians, cardiologists, geneticists, epidemiologists, nutritionists, pathologists and animal managers.113 NZP’s involvement focuses heavily on training to obtain voluntary data on blood pressure, cardiac ultrasounds and other information from its great apes during physical exams and through implanted devices. As Irus Braverman states, the role of the zoo veterinarian is now all-encompassing, drawing on medical knowledge pertaining to humans, domestic animals and animals in the wild, as ‘their expertise embodies the interrelations among all these various animals and the need for a holistic approach toward caring for all living beings, while at the same time recognizing the differences between them’.114 Moreover, with centres and programmes supporting early career researchers and specialists, NZP continues to host postdoctoral fellowships and zoological medicine residencies, as well as in situ training. Based at SCBI’s Front Royal campus, the Smithsonian-Mason School of Conservation offers hands-on, interdisciplinary programmes in conservation for a range of students, from high schoolers to professionals, in order to educate and train tomorrow’s leaders in sustaining a more biodiverse planet.115 These opportunities provide the experiences and expertise needed for interdisciplinary bridges across the paradigm of One Health, a table at which animal health experts, human health experts and ecologists all have a seat.116

At a time when much of the world is awakening to the global threat of zoonoses, COVID-19 is just one disease on NZP’s watch list. The zoo is vigilant about zoonotic diseases to ensure the health and safety of staff, visitors and collection animals: from training with occupational health staff specific to wildlife, to everyday practices with personal protective equipment and now community protective equipment, conducting research in the One Health world and closely monitoring animals as part of medical surveillance programmes. It was these types of efforts that led to San Diego Zoo Safari Park identifying SARS-CoV-2 in their gorilla troop, where testing occurred after two gorillas developed a cough.117 Less than two months later, with supportive medical treatment for some, the gorillas recovered, and experimental COVID-19 vaccines developed for dogs

114 Braverman, op. cit. (note 67).
116 Braverman, op. cit. (note 67).
and cats were administered to their orangutans and bonobos. These current events underscore that animals and their environments are the keys to understanding these types of risk to all life on Earth.

**CONCLUSION**

The history of NZP is emblematic of changes in animal care occurring across the country over the last 130 years. These changing perspectives on animal care and animal welfare reflect similar contemporaneous evolutions in human health. At the start of the twentieth century, NZP’s focus on the physical environment of its animals as the vehicle of health is reminiscent of the sanitary movement of public health in the mid nineteenth century, which promoted an antiseptic environment to combat disease. In the early decades of the twentieth century, experts in behavioural health, infectious disease medicine, pathology and veterinary medicine began to collaborate within NZP as they witnessed animal diseases and mental degradation recognizable from human patients. This focus on medical specializations to address disparate health issues intensified throughout the mid twentieth century, much as it did within increasingly diversified human medical fields. As the latter half of the twentieth century began, a period of intense focus on medical research was supported by increasing resources in NZP internal facilities. From 1941 to 1973, there were hires of permanent veterinarians alongside laboratories and facilities which rivalled some contemporaneous hospitals. Diagnostics and strict antiseptic measures began to be tempered by more holistic approaches to animal housing, sanitation, nutrition and behavioural health. By 1974, naturalistic enclosures, preventative veterinary care and nutritional plans were standards at NZP; a renewed dedication to conservation science during this time also contributed to an increase in reproductive health management. Since its centennial in 1989, NZP has increased its commitment not just to animal care, welfare and conservation, but also to scientific research in general.

Today’s NZP, like any top-tier research hospital, hosts full-time scientists, medical staff, care staff, collaborators, postdoctoral fellows and interns working to sharpen their understanding of animal health, and its consequences for our shared environment. Through digital technology and public outreach, the facilities and research that have evolved in NZP’s second century are clear: an online video of a medical exam of a young gorilla shows sophisticated technology and care by the zoo’s veterinary team, while a virtual tour of NZP’s pathology laboratory discusses One Health, zoonotic diseases and human–animal health connections. By examining the intersecting history of animal and human health at NZP, this work is better understood as part of a deeper narrative of scientific progress with far-reaching significance for the future.


ACKNOWLEDGEMENTS

The authors thank the two anonymous reviewers whose comments greatly improved this paper. We are very grateful to the Smithsonian Women’s Committee for their generous financial support of research for this study. We also thank Steve Monfort for his invaluable input on modern NZP practices, and Meredith Bastien for her comments on all aspects of the manuscript.