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REVIEW ARTICLE

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Coming to the Caribbean: Eighty-five years of rhesus macaques (*Macaca mulatta*) at Cayo Santiago—A rare nonhuman primate model for the studies of adaptation, diseases, genetics, natural disasters, and resilience

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Abstract

The Cayo Santiago rhesus macaque colony represents one of the most important nonhuman primate resources since their introduction to the Caribbean area in 1938. The 85 years of continuing existence along with the comprehensive database of the rhesus colony and the derived skeletal collections have provided and will continue to provide a powerful tool to test hypotheses about adaptive and evolutionary mechanisms in both biology and medicine.

KEYWORDS

acclimation, diseases, hurricane, knowledge model, Puerto Rico

1 | INTRODUCTION

This special issue of the *American Journal of Primatology* is a collection of articles to celebrate 85 years of rhesus macaque colony at Cayo Santiago (CS), most of them are from participants of a special symposium titled "Coming to the Caribbean—Celebrating 85 Years of rhesus macaques at CS and New Endeavors of Nonhuman Primate Research" during the 92nd annual meeting of the American Association of Biological Anthropologists (Reno, NV, April 22, 2023). The CS rhesus macaque population has operated as a significant scientific resource since their translocation to the island in 1938. The 85 years of continuing existence opens a new research direction of a long-term nonhuman primate model into the study of adaptation and resilience within the context of population history and environmental changes. The success of this introduced monkey colony has also inspired or contributed to the establishment of many other primate research centers within and outside of the United States, providing tremendous opportunities for morphological, behavioral, physiological, biomechanical, genetic, pathological, and pharmaceutical studies toward the betterment of the understanding of nonhuman primates and human conditions alike (Dunbar, 2012; Kessler & Rawlins, 2015; Wang, 2012). In addition to articles focused on the rhesus macaques, more papers on other nonhuman primates were invited to join the celebration of 85 years of CS, with topics ranging from growth and development, diseases, genetics, to animal survey and protection. These contributed papers not only showcase recent and ongoing studies in rhesus monkeys at CS and other nonhuman primates, but also prelude more exciting and innovative research projects moving forward.

Abbreviations: CPRC, Caribbean Primate Research Center; CS, Cayo Santiago; NYU, New York University.

2 | HIDDEN TREASURE IN THE CARIBBEAN: THE CS RHESUS MACAQUE COLONY AND DERIVED SKELETAL COLLECTIONS

CS (18.1564° N, 65.7342° W) is a small island (400 m × 600 m) approximately a kilometer from the eastern coast of Puerto Rico. In 1938, rhesus monkeys (*Macaca mulatta*) from India were introduced to CS to establish a free-ranging, free-of-disease, North American primate colony with a view to ensuring a stable supply for vaccine development and behavioral studies in the continental United States during World War II, which later also led to the formation of the Caribbean Primate Research Center (CRPC) (Dunbar, 2012; Kessler, 1989; Kessler & Rawlins, 2015; Rawlins & Kessler, 1986; Sade et al., 1985; Turnquist & Hong, 1989; Wang, 2012). In November 1938, under the supervision of Dr. Clarence Carpenter, 409 rhesus macaques arrived at CS from their native Lucknow, India (26.8470° N, 80.9470° E). Monkeys have been regularly provisioned since 1956, and critically, a daily census was established by Dr. Stuart Altmann, in 1956 as well—detailed life history information, including date of birth, sex, group affiliation, maternity, matriline, and date and cause of death, has been systematically collected (Dunbar, 2012), a practice that has continued uninterrupted to present day. As of January 2024, demographic data are available for 10,950 individuals.

The management practices undertaken at CS provide have provided opportunities to extract ecological influences on primate health. For example, higher levels of linear enamel hypoplasia (LEH) and odontogenic abscesses are reported before regular provisioning was introduced (Guatelli-Steinberg & Benderlioglu, 2006; Li et al., 2018) and greater long lengths reported after the switch to a higher protein diet in 1969 (DeRousseau & Reichs, 1987). Mass inoculation against tetanus in 1985 increased survivorship and lifespan expectancy, and shifted the population distribution toward an older age and increased reproductive value (Kessler et al., 2015). The population density on CS is greater than in wild populations (Boelkins & Wilson, 1972). Currently there are over 2000 individuals living on the island in seven social groups (the isthmus connecting the large and small Cayos has been under water since the 2017 hurricanes), while in the natural habitat, it might be only big enough for one natural social group with around 27 individuals. High-density populations in the wild accompany increased risk of predation, antagonism, and resource scarcity (Hernández-Pacheco et al., 2013. Though some of these effects are mitigated—increased aggression, disease transmission, and stress may accompany periods of high population density at CS (Hernandez-Pacheco et al., 2016). Artificially induced population dynamics may help us understand density fluctuations and their impact on biological health which may further be used to implement strategies in CS and similar research colonies (details of populations dynamics, see Francis & Wang, 2024a).

As an extension of the rhesus colony at CS, the CPRC skeletal collection was established in 1971 from rhesus monkeys who lived and died on CS. The collection is housed in the Laboratory of Primate Morphology at the University of Puerto Rico Medical Campus. Since 2018, the skeletal collection has been divided between CPRC and New York University (NYU) due to space constraints at CPRC. NYU's holdings, supervised by Dr. Susan Antón, are the overflow of specimens from the CPRC. In the CPRC rhesus skeletal collection, the identity, date of birth, date of death, sex and matriline is known for most of the specimens. Dominance rank and social group are known for many of the skeletons as well (Dunbar, 2012; Turnquist & Hong, 1989). The skeletons in the collection come from individuals of 26 matrilines, all born after 1950 (information of 22 matrilines with no less than 8 individuals in the skeletal collection as of March 15, 2023 in Table 1). As of January 2024, there are 2934 individual skeletons (This figure does not include the several hundred now housed at New York University—CPRC-NYU collection) (details of the structure of skeletal collections, see Francis & Wang, 2024a). One of these matrilines contains skeletons from nine generations and is still growing. The CS rhesus colony and skeletal collection have been very useful in the study of environmental and familial effects in diseases and adaptation and will continue to be a powerful nonhuman model to the study of many aspects of human conditions. Many past studies have been well reviewed and wonderfully summarized by Dunbar (2012), and here is a brief review enriched by recent and ongoing studies.

3 | ACCLIMATION AND SECULAR TREND

The skeletal collections, contextualized with known age, sex, date of birth, and familial knowledge going back over 50 years and nine generations, have allowed unparalleled studies of genetic and environmental influences on growth, development, morphology, aging, acclimation, and secular trends, while avoiding effects that may be observed in laboratory-born populations (Kohn & Lubach, 2019).

In human biology, the term "secular trend" is "applied to long-term systematic, or nonrandom, changes in a wide variety of traits in successive generations of a population living in the same territories" (Tobias, 1985, p. 347). The trend may manifest in both morphology and physiology (such as height and weight, limb proportions, acceleration or delay of growth process, time of sexual maturity, time of mating and reproduction) (Tobias, 1985). In humans, secular changes in morphology and health are indicators of environmental adaptation and changes in patterns of physical activity and diet over time (Larsen, 2015; Steckel & Rose, 2002). Similar studies could be applied to the rhesus macaques at CS (Tobias, 2012). Previous studies have shown that rhesus monkeys at CS have adapted to local seasonality in the reproduction cycle (Rawlins & Kessler, 1985), and have also demonstrated a secular trend of increasing lengths of adult long bones (DeRousseau & Reichs, 1987). Compared to laboratory animals, permanent premolars in CS rhesus erupt earlier or have a shorter period of eruption. Canines and third molars erupt later or have a longer period of eruption (Wang et al., 2016b). Differences in long bone epiphyseal closure are observed as well (Kohn & Lubach, 2019). Since 1974, the colony has been provisioned with food on a regular basis (Dunbar, 2012). Guatelli-Steinberg and

TABLE 1 Twenty-two matrilines with no less than eight individuals in the CPRC skeletal collection.

	Founder or first in collection	Matriline	Founder's year of birth	Number in collection	Total family member	Living descendants in CPRC (CS and Sebana Seca)	Note
1	CPRCMUS-00325	004	1955	67	1647	332 and 195	
2	CPRCMUS-00198	007	1955	24	27	No	
3	CPRCMUS-00275	020	1951	13	23	No	
4	CPRCMUS-00354	022	1954	129	839	90	All in Sabana Seca
5	CPRCMUS-00338	031	1955	138	363	3	All in Sabana Seca
6	CPRCMUS-00082 (Founder NIC)	058	1954	46	363	1 and 14	
7	CPRCMUS-00435	062	1953	25	164	30 and 1	
8	CPRCMUS-00373	065	1953	97	2249	306 and 302	
9	CPRCMUS-00044 (Founder NIC)	073	1951	166	2777	104 and 383	
10	CPRCMUS-00351	076	1951	158	2193	36 and 283	
11	CPRCMUS-00143	081	1951	8	34	No	
12	CPRCMUS-00129	090	1951	20	58	No	
13	CPRCMUS-00032 (Founder NIC)	091	1951	190	1369	117 and 111	
14	CPRCMUS-00063 (Founder NIC)	092	1951	86	179	No	
15	CPRCMUS-00202	106	1955	53	54	No	
16	CPRCMUS-00139	116	1953	242	3096	139 and 369	
17	CPRCMUS-01463	22	1938	84	1001	229 and 32	All in CS
18	CPRCMUS-02976	472	1971	11	102	3	All in Sabana Seca
19	CPRCMUS-00034 (Founder NIC)	AC	1954	34	167	No	Group O in DPZ (Deutsches Primatenzentrum [German Primate Center])
20	CPRCMUS-00519 (Founder NIC)	DM	1954	172	2908	363 and 360	
21	CPRCMUS-00104 (Founder NIC)	RB	1954	115	362	No	
22	CPRCMUS-00136	EA	1944	8	46	No	
	TOTAL			1886	20,021	3803	

Note: If Founders are not in the collection, the first members of these families entering the collection are listed as representatives. Total family numbers and living descendant numbers were tallied on March 15, 2023.

Abbreviations: CPRC, Caribbean Primate Research Center; CS, Cayo Santiago; NIC, not-in-collection.

Benderlioglu (2006) identified changes over time in developmental stress as reflected by the higher prevalence of linear enamel hypoplasia in CS monkeys who were irregularly versus regularly provisioned.

The timespan in which the rhesus monkeys have been exposed to the homogeneously warm conditions at CS (Latitude: 18.1564 °N) raises the possibility of whether they have acclimatized over the years. The region surrounding Lucknow, India (Latitude: 26.8470° N) experiences far greater temperature fluctuations, lower annual sun exposure and humidity than CS. An adjustment to heat exposure may be observed in the CPRC Skeletal collection via gradual population changes in body proportions and limb lengths. The CS macaques have already been separately observed adjusting their reproductive cycle to local seasonality (Hernandez-Pacheco et al., 2016; Koford, 1965; Rawlins & Kessler, 1985; Vandenbergh & Drickamer, 1974), demonstrating a secular trend of increasing long bone lengths (DeRousseau & Reichs, 1987) and of decreasing female body sizes (Blomquist & Turnquist, 2011). Secular trends of morphology and health are thought to reflect adaptation to environmental conditions over transgenerational timespans (Little, 2020). While Weinstein (2001) documented longer limb lengths in the CS macaques than in wild-shot rhesus macaques, no difference in crural or brachial indices was found, hence it was concluded that they were not acclimating to their surroundings. Our recent study demonstrated that there was a trend of decreasing body mass and long bone circumferences, suggesting an acclimation in body size and proportions of rhesus macaques, evidence for acclimation to a warmer, or in this case never cold, climate, following Bergmann's rule (Francis & Wang, 2023). If the CS macaques have been acclimating to their tropical island conditions, it may help to observe the effects on climate change on morphology, project long-term patterns of evolution in the colony, and reduce noise when cross-examining intrinsic factors on health (Francis & Wang, 2024a).

In moving to a drastically different environment almost 85 years ago it is reasonable to assume that adaptations may have arisen due to the novel conditions at CS. Such as the tropical climate, provisioned diet, high-population densities, and arboreal substrates. To identify an adaptation, we need: evidence of phenotypic change that incurs a fitness benefit, either between wild Indian rhesus macaques and those of the CS population or as a gradual change between CS generations over time. Heritable traits have been identified within the CS population, including brain size and body size (Colby et al., 2021), sexual-selective traits such as canine size (Kimock et al., 2019), yet none have been found to be under selection. The lack of selection on heritable features could suggest that many morphometric features all lie within the fitness peak for the CS population. The conditions at Cayo, such as the lack of predation and provisioned foods may have contributed towards the lack of a selection gradient on which adaptations may arise via natural selection.

Such trends across generations on short timescales at CS denote the process of intergenerational plasticity (Bell & Hellmann, 2019), or a kind of microevolution, in which opportunities are poised for future long-term studies related to adaptation and evolution, and their mechanisms, such as the Founder effect, the Island effect, the Baldwin effect, and the interactions between them. Founded by 409 individuals, this number shrank to around 70 individuals in the 1950s, with 90% of today's colony related to 15 unrelated females from this already small group (Kanthaswamy et al., 2017). The CS population thus presents an interesting case study for examining founder effects. As no individuals have been introduced to the CS island since their arrival in 1938, genetic diversity has been an area of significant research in the population. Accordingly, the CS population has been found to exhibit low levels of genetic diversity, likely due to founder and bottleneck effects (Buettner-janusch & Sockol, 1977). More recently, the population at Sabana Seca Field Station (the location of the headquarter of CPRC), which are supplied by the CS colony, were found to have 90% of the genetic variation of the California Primate Research Center and exhibited the lowest diversity among several other Primate Research Centers (Kanthaswamy et al., 2016, 2017). Although, the effects of the low number of founders at CS are believed to be mitigated by the unrelatedness of males that survived the bottleneck event and male-mediated gene flow (Kanthaswamy et al., 2017). The influence of increasingly low levels of genetic diversity in the CS skeletal collection thus warrants more studies. Moreover, reduced body weights and statures may relate to the Island effect (Francis & Wang, 2023). Though the population density has fluctuated over the course of its history, there has been a sharp rise overall. The relative lack of roaming area, despite adequate resources due to provisioning, may have contributed to secular trends in morphology observed in the colony and thus so has the island effect. Finally, the Baldwin effect was first proposed by James Mark Baldwin in 1894. It refers to the behavioral learning and eventual genetic assimilation of a learned trait. Incorporating a mix of plastic and natural selection, the effect has been seen as a reconciliation between Darwinism and Lamarckism (Simpson, 1953).

The Baldwin effect has been implicated in the evolution of human musicality (Podlipniak, 2017), stone tool use (Corbey, 2020), and language (Christiansen et al., 2011). There is no current evidence for the Baldwin effect in the CS population. It is plausible that it has, however, the translocation of the rhesus macaques to CS presented a host of novel environmental conditions with which new learnt behaviors may arise. For example, the CS population is not subject to predators, many questions could be framed, such as: Have the instincts associated with predator avoidance been lost in the CS macaques? Have the high-density population numbers sparked new/enhanced cooperative behaviors or channeled predator-avoidance strategies to interindividual and intergroup conflicts? Morphological and behavioral adaptation and evolution might lead to the rise of a new geographical variant of rhesus macaques (Caribbean variant) (more in Section 5).

4 | PATHOLOGICAL STUDIES OF THE SKELETAL COLLECTION

The anatomy and physiology of rhesus macaques is highly similar to that of humans, hence their ubiquity in biomedical research and translational medicine (Chiou et al., 2020). In lieu of this, some of most devastating osteopathologies are well represented in the CRPC skeletal collection. These include oral pathologies, such as periodontitis (Ebersole et al., 2019; Gonzalez et al., 2016; Wang et al., 2016a), odontogenic abscesses and cysts (Li et al., 2018), and caries (Wang et al., 2016b), age-related diseases such as osteopenia/porosis (Cerroni et al., 2000, 2003; Grynpas et al., 1989; Kessler et al., 2015; Turnquist et al., 2012), osteo- and inflammatory arthritis (Lim et al., 1996; Rothschild et al., 1997, 1999), as well as osteomyelitis, osteosarcomas, and bony fractures. Interestingly, some diseases demonstrated familial aggregation (Ebersole et al., 2019; Francis & Wang, 2024a). For example, though generally the extent and severity of periodontitis are age related, certain matrilines are more susceptible, even in aged individuals (Ebersole et al., 2019), demonstrating different levels of resilience across different matrilines.

Beyond the most pervasive and destructive pathologies, the CPRC skeletal collection features important congenital defects as well (Rawlins & Kessler, 1983), nonmetric features (Cheverud & Buikstra 1981a, 1981b, 1982; Francis & Wang, 2024b; Richtsmeier et al., 1984; Wang et al., 2006), and a range of other dental abnormalities (Wang et al., 2016b). As rhesus macaques undergo natural senescence periods, form spontaneous diseases in a free-ranging environment, and are associated with known demographic and familial information, they are poised to develop a viable biomedical model for studying bone health and diseases, specifically to further understand the heritability of skeletal health conditions, in addition to environmental impacts, such as nutrition/provision, population dynamics, and natural disasters (i.e., hurricanes) (Zhao et al., 2021, 2023; Francis & Wang, 2024a). A comparison of those who experienced differing nutritional qualities for the most common oral pathologies has demonstrated that periodontitis decreased with increasing nutritional quality, while antemortem tooth loss and periapical cavities showed a trend of increase with better nutrition (Francis & Wang, 2024a). This trend may reflect a similar phenomenon in humans since the rise of agriculture and postindustrial revolution in which a shift to softer foods has reduced the size of the mandible and thus the space for teeth to fully erupt and align (von Cramon-Taubadel, 2011).

5 | GENETIC STUDIES

The CS social groups provide a unique opportunity to study population genetics in a naturally formed population. Since their introduction in 1938, after experiencing some turbulent early years, including hardships in sustenance, shifts in funding and management, and most recently devastating hurricanes, the colony has persisted and progressed, gradually. It is now poised to be a "Caribbean variant" of rhesus macaques.

Detailed life history data have been collected since 1956, including date of birth, sex, group affiliation, maternity, matriline, and date and cause of death. For females, social group membership is based on matrilines, and each matriline includes a female, her adult offspring, and their juvenile and infant offspring (Kanthaswamy et al., 2017; Kessler & Berard, 1989). Males migrate from their natal social group to join a different social group as they reach adulthood and may change social group multiple times throughout adulthood (Kanthaswamy et al., 2017; Sade, 1972). Several social groups have undergone lineal fission, which generally occurred within matrilines (Chepko-Sade & Sade, 1979). Dates of group fission and resulting group memberships are all recorded. Genetic differences between social groups are based on differences between group founding members, natural selection, male migration, and genetic drift. Differences among groups have been found for blood antigens (Cheverud et al., 1978; Duggleby, 1978), skeletal morphology (Cheverud & Buikstra, 1978; Cheverud & Cheverud, 1981; Kohn & Bledsoe), yet as expected, groups with shorter time since fission are more similar than those that have been separated for a longer period.

In addition to census data, DNA fingerprinting of the CS colony began in 1989 (Krawczak et al., 1993) and is used extensively to identify paternal and maternal relationships. This facilitates analyses of both paternal and maternal effects, such as dominance rank, age, and reproductive success on observed characteristics (Widdig et al., 2016). The addition of paternal, as well as maternal relationships, will expand the richness of the available genealogical information available, and further expand the types of studies that are possible. More recent techniques have leveraged maternal and paternal information to generate animal models able to investigate selection and heritability on body and brain size (Colby et al., 2021), dental dimensions (Hardin, 2019), sexual-selection characteristics (Kimock et al., 2019), maternal effects (Blomquist, 2013), social attention (Watson et al., 2015), and interbirth intervals on mortality (Lee et al., 2019) in the CS macaques. Moreover, intriguingly, the results of several genetic studies suggest that mating patterns within CS have resulted in inbreeding (Duggleby, 1978; Kanthaswamy et al., 2017; Widdig et al., 2017). The rate of golden hair, 52× the rate observed in the wild, has been considered visual evidence of inbreeding in the CS population (Rawlins & Kessler, 1983; Widdig et al., 2016). In tigers with diminished population sizes and increasing inbreeding chances, the golden-colored hair of certain individuals was found to be resulted from an autosomal recessive gene (Xu et al., 2017). The increasing prevalence of golden hair at CS might have a similar molecular mechanism. In the future, numerous traits related to growth, development, pathology, variation, and selection have yet to be elucidated using the available pedigree and genetic information at the CS colony.

6 | HURRICANE EXPERIENCES: IMPACTS AND RESILIENCE

The translocation of the CS rhesus macaques not only exposed them to a more tropical landscape but to one that periodically experiences devastating hurricanes. At least 56 major hurricanes have passed through Puerto Rico, a Caribbean area under constant threat of hurricanes, since 1780. Since their introduction to the island, four major hurricanes at Category 3 or higher have hit CS: Hurricane Hugo (September 18, 1989), Hurricane George (September 21, 1998), Hurricane Irma (September 6, 2017), and Hurricane Maria (September 20, 2017). Hurricane Maria led to loss of vegetation and total destruction of water and the feeding corrals, resulting in food shortages and increased sunlight/ultraviolet exposure due to defoliation damage. (The feeders and corrals were reinstalled 1 month later by NSF Emergency support through the efforts of Susan Antón and James Higham.) Mental health impacts are reported in humans who experienced such events (Scaramutti et al., 2019; Schwartz et al., 2017). In nonhuman primates, mortality patterns have reportedly increased, as has diet and behavior changed (Behie & Pavelka, 2005; Milton & Giacalone, 2014; Schaffner et al., 2012). The long-term impact of hurricanes on the health of primates has never been fully studied. According to Motes-Rodrigo et al.'s modeling, hurricane induced increasing social connections would enhance disease transmission risk at CS (Motes-Rodrigo et al., 2023). Some of the most notable studies on hurricane impact have so far been conducted on the CS macaques—detailing trends of decreased fertility (Morcillo et al., 2020), delayed reproductive debut (Luevano et al., 2022) and increase in sociality (Testard et al., 2021) postimpact. Our study also indicates that hurricane experience would lead to the increase in the prevalence of systemic diseases, decrease in bone mineral density in young adults, in addition to the delayed eruption of the primary dentition (Francis & Wang, 2024a). Different matrilines and social groups might have different levels of resilience, which might be overshadowed by human interventions (i.e., provision and vaccination). Nonetheless, these findings suggest the long-term negative impacts in the juvenile individuals that experienced extreme climate conditions, yet these impacts on longevity, pathology, endemics, mating and reproductive strategies are warranted in future studies.

7 | UNIQUENESS, MORE OPPORTUNITIES, AND LIMITATIONS IN THE USE OF CS COLONY AND SKELETAL COLLECTIONS FOR STUDYING HUMAN CONDITIONS

The uniqueness of the CS colony and its derived skeletal collection lies in (1) the depth of information known about each individual; (2) the degree of completeness of the skeletons in the collection—full skeletons in a well preserved condition, (3) the fact that the specimens are from free-ranging (not caged) rhesus monkeys of the same colony, (4) the natural development periods and senescence of individuals in this colony (i.e., they are spontaneous, not induced experimentally), and (5) the existence of a soft tissue collection associated with some of the skeletons, allowing in-depth genetic studies. Thus, the CS colony and the derived skeletal collection offer a rare nonhuman primate model for the studying of human conditions, especially health and diseases.

A searchable and computer-interoperable Knowledge Model, CSViewer that integrates CS census and skeletal data (special developmental and pathological traits such as premature synostosis, fractures, osteoporosis, osteoarthritis, etc.) has been developed (Zhao et al., 2021, 2023). In addition to the interactive tools that support manual search and analysis functions, intensive computer techniques (such as classification, association rules) will be used to discover previously unknown associations from the rhesus family data. Software interfaces will be provided to allow researchers to extract and prepare data from the rhesus database to run machine-learning methods and test their hypothesis. This bone database and knowledge model will provide a strong tool for investigating bone health conditions within the context of population dynamics and family history. Patterns and new knowledge obtained will be fed back to enrich the library and made available for secondary data analysis to the academic communities. Doing so would allow comparisons between human and rhesus conditions to test specific hypotheses, such as on the connection between skeletal health with high parity, and on the possible negative relationship between osteoporosis and osteoarthritis (Havill, 2003; Kessler et al., 1986).

However, it might be kept in mind that there are limitations applicable to any study employing skeletal/nonhuman primate populations to model human health. For example, where observable skeletal pathology may be a sign of ill-health, the osteological paradox emphasizes that the ultimate sign is death itself (Wood et al., 1992). In the most fragile individual, pathology may not have had time to impart any skeletal marker of illness whereas those with signs of pathology have at least survived long enough for it to register. Additionally, certain pathologies will not leave a marker under any circumstances. The second point refers to the gap in applicability between a human and nonhuman primate. While rhesus macaques are key step in the development of many modern therapeutic and medicinal innovations, differences in genetic affinity, locomotion, sociality, diet, morphology, and environmental factors all play a role in limiting the translational potential of rhesus macaques as a human health model. Other limitations often leveled at the colony include provisioned foods, lack of predators, uncommonly high population densities, and medical interventions. Whereas these all may be drawbacks against nonhuman primate wild-like modeling, these are features generally shared by many modern human populations. For instance, provisioned food and lack of predators could mirror our ease of access to food and relatively sedentary lifestyles. Humans are increasingly concentrated in high-density cities as population numbers rise (Francis & Eller, 2022). Likewise, medical interventions extending lifespans in humans, they have also done so in the CS macaques. With limitations kept in mind and well controlled, research findings would benefit the studies fundamental biological mechanisms that underlie bone development and skeletal integrity and health, and the relationships between the environment, genetics, and health risks and their applications to human conditions.

8 | CONCLUSION

The CPRC maintains one of the most important and valuable primate colonies in the world. Equally, the CPRC skeletal collection represents one of the most important skeletal research resources in the world, and thus has a high potential to yield significant morphological, pathological, and genetic data on the importance of environment and family lineage to bone and joint diseases, as models for human conditions. Along with the comprehensive database of rhesus colony health history and its environment, the collection will continue to operate as a powerful tool to test hypotheses about adaptive and evolutionary mechanisms in both biology and medicine, as well as the long-term negative impact of hurricanes on health of a nonhuman primate to ascertain the health risk of hurricane experience during the early stage of the life.

AUTHOR CONTRIBUTIONS

Qian Wang: Conceptualization (lead); funding acquisition (lead); writing—original draft (lead); writing—review and editing (lead). **George Francis**: Writing—original draft (supporting); writing—review and editing (supporting).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request. The access to raw census database needs to be granted by the Caribbean Primate Research Center. An interdisciplinary team led by Qian Wang, funded by NSF (RIDIR 1926402, 1926528, 1926481, and 1926601), aimed at integrating related data of rhesus macaques at Cayo Santiago on different aspects for the studies of growth and development, acclimation and adaption, and health and diseases as a nonhuman primate model. This project has resulted in a comprehensive database with innate and added analytical tools, CSViewer, a unique Knowledge Model which enables data mining, data analysis, and modeling support for hypothesis-based investigations based on census information and historic record of the monkey colony, and metric and nonmetric data collected from derived skeletal collections. This database and knowledge model has been introduced in a workshop, "CSViewer for Analysts—A big data approach to Cayo Santiago rhesus macaque colony: A workshop on a software application to generate user-friendly interface and appropriate powerful data analytical tools" during 2024 American Association of Biological Anthropologists Annual Meeting, March 20, 2024, Los Angeles. This knowledge model has been released to the workshop participants for test run and evaluations, and the refined program will be released to the public and scientific community upon the conclusion of this project before September 2025. Because monkeys have name (tattoo) and vital information (birth and death dates, sex, mother's name, and so on), and are hence treated as human patients and protected by HIPPA per CPRC policies, a unified code name will be used for individuals in the knowledge model, except key matriline founders' names for lineage identification and search. Rich documents and images collected by Dr. Matthew Kessler, former Director of the Caribbean Primate Research Center, recording the history of Cayo Santiago rhesus colony and CPRC will be permanently stored in a university or museum archive.

ETHICS STATEMENT

The research was noninvasive. For research work, we obtained permission to collect data based on skeletons from Caribbean Primate Research Center.

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