Chimpanzee life history patterns and behavioral changes with age

A thesis by

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Havercamp, K., Watanuki, K., Tomonaga, M., Matsuzawa, T., & Hirata, S. (2019). Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018. *Primates*, 60, 525–535. https://doi.org/10.1007/s10329-019-00755-8

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Chapter 1

General Introduction

Captive populations of animals around the world are rapidly aging. This is especially the case for chimpanzees (*Pan troglodytes*), the closest living evolutionary relatives of humans along with bonobos, with whom we share various biological, cognitive and behavioral traits. Chimpanzees have been held in captivity across the world for roughly a century, and were initially captured in Africa and imported into countries such as American and Japan for entertainment purposes. From the 1970's, chimpanzee importation surged and hundreds of individuals were taken from the wild with the purpose of using them as biomedical research subjects in order to better understand and cure human diseases such as AIDS and hepatitis (Bailey 2010). At the same time, captive breeding programs were initiated to increase the number of chimpanzees available for research and entertainment such as placement in zoos. However, importation was stopped in the early 1980's following the ratification of the Convention of the International Trade in Endangered Species of Wild Fauna and Flora (CITES) and invasive biomedical research using chimpanzees was ended around three to four decades later varying between countries, for example in 2006 in Japan and in 2015 in America (Grimm 2017; Hirata et al. 2020). Due to the unique importation history of chimpanzees, as well as falling birth rates and advances in medical care (Neal Webb et al. 2020), captive populations around the world will soon be made up of a majority of elderly individuals.

Due to the close evolutionary relationship between chimpanzees and humans, their life history patterns (i.e., series of events undergone by an organism such as birth, development, aging and death) and behaviors have been studied to reveal important insights not only about

them, but also into the evolution of human traits and behaviors. Life tables provide crucial data such as mortality and longevity rates across an animal's lifespan (i.e., from birth to death). However, robust life tables do not exist for some species as it is not always possible to collect precise data for individuals over their entire lifespan, especially for long-lived animals such as chimpanzees. The longevity and mortality of wild chimpanzees and human hunter-gatherer populations have been compared to reveal insights about human senescence and life history patterns (e.g. Hill et al. 2001; Emery Thompson et al. 2007; Muller & Wrangham 2014; Wood et al. 2017). However, life history data on captive animals is often unavailable to researchers and is maintained and kept by zoo staff or studbook managers. This information is necessary to be able to compare the longevity and mortality patterns between captive and wild individuals, as well as with human populations. Of the life tables which exist for captive chimpanzees, none are robust and all are outdated (Courtney & Santow 1989; Dyke et al. 1995; Littleton 2005). Due to the relatively short history of these populations at that time and individuals having had yet to live out their entire lifespan, reported life expectancy estimates were either derived from modelled data (Dyke et al. 1995) or were not reported due to life tables reaching a limited age (Courtney & Santow 1989; Littleton 2005). Thus, fundamental information on the mortality patterns and longevity estimates of captive chimpanzees is missing.

Physical, cognitive and behavioral changes that occur with aging in primates is a topic of growing interest, likely in part due to their increasing presence in captivity. While many studies exist exploring physical and cognitive changes in aging chimpanzees (e.g. Lacreuse et al. 2014; Emery Thompson et al. 2020a; Emery Thompson et al. 2020b; Hopkins et al. 2021), few studies examine changes in their behaviors as they grow old (Baker 2000; Rosati et al. 2020). Understanding behavioral changes that occur during the aging process is particularly difficult

due to a lack of longitudinal data, which is in part due to a relative lack of research focus until recently. However, just as research on human aging across a range of topics is of critical importance to our health and welfare, it is important that we understand the aging processes of other animals as well in order to provide the best quality of care for them throughout every life stage. In the case of primates, what we can learn from them will also provide insights into the origins of healthy human aging.

Together, these various limitations pose challenges in understanding the life history and aging patterns of animals. Using a unique national open-source database and existing longitudinal data, some of these challenges are overcome in the following enclosed chapters. Given the rapidly changing population dynamic, understanding the life history patterns of chimpanzees, including mortality risks over the lifespan and longevity estimates, as well as behavioral changes they may experience with aging will be crucial knowledge for a full understanding of their biology and behaviors. This information will also contribute to successful captive population management and welfare planning.

This dissertation aims to describe the life history patterns of captive chimpanzees as well as examine behavioral changes, specifically in sleep, that occur with aging. In Chapter 2, long-term data on 821 individuals in Japan spanning nearly a century held in the open-access Great Ape Information Network (GAIN) database is used to build the first robust life tables for captive chimpanzees and to describe their life history patterns. Specifically, the life expectancy, mortality risks, infant mortality patterns, and seasonal mortality patterns of chimpanzees living in Japan are examined for the first time. This research provides foundational information to be used for chimpanzee management and welfare planning not only in Japan, but across the world in

various captive environments, and is a resource for future comparative studies between populations and across species.

Chapter 3 uses these data as part of a cross-country comparative study, where the longevity and mortality patterns of the historical captive chimpanzee population in Japan are compared to those in America. This comparison aims to provide the most up-to-date and robust life tables thus far, while exposing similarities or differences in survival patterns between the two regions, especially between the sexes. Additionally, captive chimpanzee survival patterns are compared to those of wild-living chimpanzees. These life tables are available online as open-access and will be valuable resources for future cross-regional, between-species and within-species comparative studies.

Chapter 4 is an examination of behavioral changes that may occur with aging in a captive chimpanzee population, specifically in their sleep patterns. Following human sleep studies where decreasing quality of sleep with aging is repeatedly described (e.g. Mander et al. 2017; Li et al. 2018), the aim of this chapter is to examine the potential changes in sleep patterns of chimpanzees at Kumamoto Sanctuary in Japan using longitudinal data. By comparing the sleep patterns of the same individuals over a decade period, it is possible to explore whether the changes humans' experience in their sleep patterns as they age are a more recently evolved phenomenon or if this may be an evolutionary conserved behavioral change. In addition to this, whether changes in chimpanzees' behavioral patterns are found to occur with natural aging will provide essential information which can be used to improve the welfare conditions of elderly individuals.

By integrating chimpanzee life history data and longitudinal behavioral data, this research not only contributes to a deeper understanding of chimpanzee biology including their mortality

and longevity patterns, but also how aging influences their behaviors which may change throughout their lifetime. Given that the aging captive population will rapidly increase in the years ahead, this information will be crucial for successful population management and welfare planning. Together, these studies reveal the robust life history patterns of captive chimpanzees for the first time, provide data accessible for future comparative studies across populations and species, and shed insight into chimpanzee aging as well as why humans age the way we do.

Chapter 2

Longevity and mortality of captive chimpanzees in Japan from 1921–2018

2.1 Introduction

Due to humans' closely shared evolutionary history with chimpanzees, their longevity, mortality and reproductive patterns have been studied to better understand human life history evolution (e.g. Hill et al. 2001; Emery Thompson et al. 2007; Muller & Wrangham 2014; Wood et al. 2017). Mortality data from five wild chimpanzee study sites including Gombe, Taï, Kibale, Mahale and Bossou indicate that life expectancy for both sexes at birth is less than 15 years (Hill et al. 2001). Individuals reaching age 15 survive around 15 years longer, leading to a life expectancy of around 30, with males experiencing higher adult mortality than females (Hill et al. 2001). The maximum longevity of a wild chimpanzee reported in 2017 is an estimated 66 years at Ngogo in Uganda (Wood et al. 2017). Compared to human hunter-gatherers, wild chimpanzees experience around half the life expectancy at birth and less than half post-adulthood (calculated from age 15), and their mortality rate is seven times higher between 30-35 years of age than that of the Ache (Kaplan et al. 2000; Hill et al. 2001). However, chimpanzees living in Ngogo, an environment with high fruit availability, have an average life expectancy at birth more comparable to that of hunter-gatherers, of 32.8 years (Wood et al. 2017).

Life history statistics are easier to obtain for captive chimpanzees compared to their wild counterparts, yet robust data are missing in the literature. The first life table for captive chimpanzees was published nearly 30 years ago and included 65 individuals (Courtney & Santow 1989). The authors were only able to calculate mortality probabilities up to age 30 due to the young population at that time. Since Courtney and Santow (1989) two additional captive

chimpanzee life tables have been published in scientific journals, and both are now relatively outdated (Dyke et al. 1995; Littleton 2005). Calculations from observed data valid through 1995 reported that females could expect to live 23.1 years, whereas a fitted model estimated 44.9 years (Dyke et al. 1995). Other studies have gathered life table data from databases such as Species360 to investigate animal longevity, however the chimpanzee cohort data analyzed were also missing recent data (Tidière et al. 2016). Thirteen years have passed since original data on captive chimpanzee mortality or longevity have been published or updated, not including studbooks which are more commonly shared privately amongst zoo communities, and existing life tables are relatively small for demographic analyses. The accuracy of life history calculations depends on the length of time a population has been maintained and tracked, and thus a more current and robust life table is necessary to improve our understanding of captive chimpanzee demographic life history patterns.

Animals living in captivity may experience different mortality rates, as well as reproductive patterns, from those living in the wild under more natural conditions. Whether or not captive chimpanzees outlive their wild counterparts is unclear. While in some settings wild adult chimpanzees experience higher overall mortality risk than captive living individuals (Courtenay & Santow 1989; Hill et al. 2001), in others captive males and females live six and seven years less, respectively, however the number of individuals included in this study were few (Tidière et al. 2016). Extended survival in captivity has been explained by the high level of care animals receive (e.g. high quality and various nutritional food items, health care) and lack of predators, however individuals may also experience negative effects such as human-induced illnesses, a lack of exercise, over feeding (which could lead to health issues such as diabetes or heart disease) and increased intraspecific violence due to living in a confined space (Hill et al.

2001; Kohler et al. 2006). Also, captive conditions may vary across facilities (e.g. zoos, sanctuaries, research institutes) which might influence life history parameters, something which has been so far difficult to explore.

The goal of our current study was to utilize the 97 years of data included in the Great Ape Information Network (GAIN) database to examine the demographic life history patterns of captive chimpanzees in Japan. Initiated in 2002 by Tetsuro Matsuzawa and colleagues, GAIN was developed to counteract the shortage of captive primate data with the goal to provide accessible and real-time data on all non-human apes (henceforth apes), great and small, previously or currently living throughout Japan (Matsuzawa 2016). The three main aims of GAIN include 1) the promotion of non-invasive scientific research through a real-time utilization system of bio-resource samples, such as a dead body, 2) assistance in primate population management and 3) promotion of animal welfare and facilitation of networks between zoo staff and researchers. Historical data on apes in GAIN date back to 1921, when the first chimpanzee arrived to Japan (Watanuki et al. 2014). Current to March 11, 2019, the highest number of individual data recorded in the GAIN database is 1,017 chimpanzees, followed by 589 gibbons, 255 orangutans, 122 gorillas and six bonobos. At the time of writing, 307 chimpanzees, 176 gibbons, 46 orangutans, 21 gorillas and six bonobos reside in Japan.

Using the database, we produced a robust life table to better understand demographic life history patterns including age-specific mortality rates and calculated the life expectancy and maximum longevity of captive chimpanzees; this is the first such report using available data on chimpanzees in Japan. We also investigated whether patterns in death seasonality exist, which to our knowledge has never been determined for a captive chimpanzee population, and attempted to answer whether or not life expectancy in captivity has increased over time. Finally, we discussed

the existing literature on both wild and captive chimpanzees to examine how life history patterns differ across environments and populations, especially in comparison to the captive population in Japan.

2.2 Methods

2.2.1 Data

We obtained records on every chimpanzee who has previously lived or currently lives in Japan from the open-access GAIN database (https://shigen.nig.ac.jp/gain/). The majority of individuals have a detailed record of their entire lifespan available to users including information such as date of birth and death, sex, birth place, current location, any dates and locations of transfer, reproductive history, family pedigree, early life experiences and a brief physical and personality description. Current to March 11, 2019, information on 1,017 chimpanzees existed, more than any other species in the database. At the time of writing, 307 were living in 49 different facilities including zoos, research institutions and sanctuaries. There is only one sanctuary in Japan, Kumamoto Sanctuary, however this facility was owned by a biomedical research company until it was taken over by Kyoto University in 2011 (Morimura et al. 2011); a total of 193 chimpanzees have spent either all or some part of their life there (Fig. 2.1). More than 76 additional individuals were housed across eight biomedical research institutions at some point during their lives, at least 26 in two research institutes, and the remaining majority in a zoo, park, or center. Although likely an underestimation, 33 individuals have been documented as privately owned and an additional 24 as unknown. This history of this population has been described in more detail by Watanuki et al. (2014), Ochiai et al. (2015), and in English by Hirata et al. (2020). These data were entered into PopLink 2.4 (release date Dec 15, 2012;

https://www.lpzoo.org/conservation-science/projects/poplink), a captive population management software (Faust et al. 2012a). PopLink data were imported into PMx (http://www.vortex10.org/PMx.aspx) for the production of the current age-sex composition chart (Ballou et al. 2010).

2.2.2 Age estimation

Only following 1926 were definite birth dates recorded for individuals born in captivity. The recorded year of birth of all chimpanzees who were born in the wild or have an unknown origin is an estimate. In the majority of cases, individuals were allocated an estimated year of birth based on morphological features and age-typical behaviors at the time of importation. Underestimation of age may have occurred more frequently in earlier years of importation due to the lack of detailed knowledge about chimpanzee development. Of all individuals in the database, 394 (39%) did not have a definite year of birth on record. Individuals recorded as having an estimated year of birth or death were allocated a birth or death day of July 1st following instructions set by the developers of PopLink to use the middle date of the estimated year (Faust et al. 2012b). The date estimate for such cases was entered as "Year" within the software, which allows for the acknowledgement of less precise dates however uses the specified mean transaction date to calculate age-specific demographic parameters. Individuals with no known or estimated date of birth, capture, departure or death were not included in analyses.

2.2.3 Lost to follow-up (LTF)

In total, 173 chimpanzees documented by GAIN were lost to follow-up (LTF) cases, 125 of which were exported out of Japan to another institution. The remaining 48 remained in Japan

but were no longer tracked. The first documented exportation was in 1931 when a privately owned, American born individual was believed to be brought back to America. The most recent exportations were in September 2015, when three chimpanzees were moved to Malaysia. Other LTF cases included known deceased individuals without any recorded year of death estimate. Individuals with available birth and LTF data were included in the life table, but censored at the age of departure; rather than assumed death they simply disappear from the table in the year they left Japan.

2.2.4 Infant survival rates

Infant survival rates were calculated as the number of surviving animals beyond the first year of life as a proportion of all births using two methods, the first including and the second excluding stillbirths. Only captive born individuals were included in infant survival rate calculations because they have definite known dates of birth, unlike individuals who come from a wild or unknown origin. All but three individuals born in captivity abroad were brought to Japan after having reached at least one year of age, thus were not included in infant survivorship calculations. The majority of wild born chimpanzees were also estimated to be older than one year at the time of arrival to Japan (n=27 estimated as under one).

2.2.5 Life table

Life tables can provide age-specific survival, mortality and fecundity rates of a population. Cohort, or generation, life tables include only individuals born in the same (ideally relatively short) time period, following them through their entire lifespan and thus require a very large sample over a specific period of time. In contrast, synthetic life tables incorporate data

from all available study years. The synthetic life table presented in this paper was produced in Excel, using data exported from the population management software PopLink v2.4. The life table contains historical event information on every known individual in the population, utilizing their estimated or certain date of birth, date of entry into the population, exit out of the population and/or death (Faust et al. 2012b). Individuals were thus added to the table either in the year of birth or immigration (here, importation) and removed from the table in the year of death or emigration (exportation or LTF) out of the Japanese population. Those still alive on March 11, 2019 were considered closed. Individuals with an unknown birth date estimate or those deceased with an unknown death date were not included in the life table due to the inability of calculating age (Faust et al. 2012b). Individuals born alive and surviving to at least 1 day of age or living in Japan during any period ranging January 1, 1921 to March 11, 2019 were included in the life table, resulting in 821 (479 females, 342 males) chimpanzees of 1,017 for whom sufficient data existed. Birth and death estimates existed for ten individuals of unknown sex, but they were not included in the life table.

2.2.6 Death seasonality

To investigate death seasonality, the number of individuals who died in each month across all years was counted using the population management software PMx (http://www.vortex10.org/PMx.aspx) with data imported from PopLink.

2.3 Results

Of the 1,017 individual chimpanzees documented in the GAIN database, just over half (n=537, 53%) were recorded as deceased and nearly one fifth (n=173, 17%) as lost to follow-up

(LTF; exported out of Japan), leaving 307 (30%) chimpanzees who were alive in Japan at the time of writing. Females outnumbered males and made up over half of the historical population (n=574, 56% and n=405, 40%, respectively), and 38 (4%) individuals were of unknown or undecided sex. The majority of individuals were born in captivity (n=535, 53%), almost one third in Africa ("wild born"; n=302, 30%) and many originated from an unknown birthplace (n=180, 18%). Individuals with a wild or unknown origin were provided an estimated year of birth and thus their age at death or current age is not precise as it is for those born in captivity (median age at import: 2.0 y; average: 2.5 y; range: 1 m–19.24 y; st. dev: 1.9 y). The number of wild born individuals living in Japan peaked in 1984 at 170. Since 1992, captive-born chimpanzees have outnumbered those born in the wild.

2.3.1 Current age-sex composition

Age-sex charts illustrate the demographic composition of a population at a given time. Due to the long history of holding chimpanzees in Japan, a bias towards the existence of more young individuals than old did not exist. The current demographic composition showed the opposite pattern, that of an aging population, however with only 23 individuals alive between 30 and 34 years of age compared to 58 chimpanzees between 25 and 29 years and 45 between 35 and 39 years (Fig. 2.2). Two of every five (40%) chimpanzees alive in Japan were 33 years of age or older (may be considered "elderly") and over half (63%) were above 25 years old.

2.3.2 Infant survivorship

Of the 535 individuals born in captivity, 502 were born in Japan. The birth of the first chimpanzee in Japan was on July 22, 1940 at the Osaka Tennoji Zoo, but the infant was stillborn.

Of all captive births in Japan, nearly one in every six (n=72, 14%) infants were delivered stillborn ("non-live" birth). The number of stillbirths has irregularly increased over the decades, from 13% (n=7) of all births in the 1970's, to 10% (n=10), 16% (n=27) and 15% (n=16) in the following decades, and most recently 20% (n=11) from 2010 to March 2019. The remaining 430 infants (86% of total births) were born alive ("live" birth) and 421 lived beyond one day of birth. Four fifths of all chimpanzees born in Japan survived past one week of age (n=402, 80%) and just over two thirds reached or surpassed their first birthday (n=341, 68%) (Table 2.1). Causes of death for individuals who died on the day or soon after birth include aggression from other individuals, illness, neglect and accidental injury. In total, 161 chimpanzees died before reaching their first birthday. Excluding non-live births, the number of chimpanzees who died before reaching one year of age decreases to 89 infants. Considering all births in Japan, the first-year infant survival rate for chimpanzees was 68%, but including only live births this increased to 79%. The one-week survival rate also increased when only live births were considered, from 80% to 94% (Table 2.1).

2.3.3 Maximum longevity

The longevity record for chimpanzees in Japan was set on January 15, 2019 when the longest living individual, a wild born male named Jhonny estimated to be 68 years old, passed away at the Kobe Oji Zoo (brought to Japan in 1952 at estimated age of 2 years, +/- 1 y age estimate). The second oldest individual in GAIN records was Mimie, a wild born female who passed away at the Tama Zoological Park in 2015. She lived to an estimated age of 59 years, nearly a decade younger than the oldest male (brought to Japan on March 9, 1958 at estimated

age of 1.7 years, +/- 1 y age estimate). While ten females reached or surpassed the estimated age of 50 (Table 2.2a), only five males did (Table 2.2b).

2.3.4 Life table

Despite having lived at different times and in different facilities across Japan, all individual data were combined in a single, synthetic life table to provide an overview of mortality rates in captivity including as many available data as possible, but excluding stillborn individuals (Table 2.3). The data contain 9,334 observation years on females including 243 deaths, whereas about a third less, 6,289 years and 161 deaths, exists for males. Females experienced a higher mortality risk (q_x) in the first year of life than males, at 22% and 15% respectively (Table 2.3). From infancy to adulthood, females experienced a consistently slightly lower survival probability compared to males, and at age 30 they reached a 43% and 44% chance of survival from birth, respectively (Fig. 2.3). When calculated from one year of birth ($l_x[1y]$), females and males experienced nearly the same survival rate until age 29 where males dropped below females, especially from 36 to 43 years (Table 2.3). Life expectancy at birth including individuals who survived past one day was 26.3 years for females and 30.3 years for males. Including only individuals who reached or surpassed their first birthday, female and male life expectancy increased to 32.4 and 34.7 years, respectively. Kaplan-Meier estimates indicated that female and male survival curves were not statistically different ($X^2 = 0.2114$, df = 1, $p = 0.6467$).

2.3.5 Life expectancy over time

It was not possible to produce yearly abridged life tables from GAIN data due to the small number of births each year, so in order to investigate whether life expectancy changed over

time we compared the median age of individuals who died in a particular year to the median age of individuals alive that year (excluding all individuals below one year of age due to high infant mortality). This allowed us to 1) explore whether median life expectancy was increasing over time and 2) verify whether or not potentially increasing lifespans were an artefact of a greater number of old chimpanzees existing. We found that median life expectancy increased over time, especially over the past few decades, however increasing lifespans may be an artefact of a greater number of older chimpanzees existing (Fig. 2.4). Nearly twenty years ago the population was made up of individuals aged around 15 and median age at death was around 20 years; today the median population age is around 25 years and age at death is 34. The median age of chimpanzees alive each year in Japan is still increasing and has not yet levelled, likely because many were brought to Japan in the 1980's and have not yet reached their longevity potential.

2.3.6 Death Seasonality

We found a seasonal effect on the chimpanzee death rate. Chimpanzees in Japan were more likely to pass away in the winter months (Dec–Feb) than in any other defined season ($n=108$; Chi-square test, $p < 0.001$). In comparison, 68 individuals died between March and May, 75 between June and August and 62 between September and November (Fig. 2.5). Data excluding neonatal deaths (defined as death before one year) were analyzed due to the diverse causes leading to newborn deaths, however a similar pattern was observed in data including neonatal deaths.

2.4 Discussion

In this study, we present a life table featuring data that span nearly a century and include 821 captive chimpanzees who have either previously lived or currently reside in Japan. We wish to make these data available for future comparative investigations into animal life history patterns. To do this, we utilized the Great Ape Information Network (GAIN), an openly accessible database containing the life history information of all apes in Japan. The robust life table and longevity and mortality statistics presented here will hopefully contribute to and broaden our understanding of captive chimpanzee demographic life history patterns.

A low survival period the year following birth is observed across many animal species (Kohler et al. 2006). Courtenay & Santow (1989) reported that 63% of live-born infants in the Taronga Zoo population survived the first year of life, but this was later lowered to 60% (Littleton 2005). Dyke et al. (1995) described an 80% to 86% survival rate in three major breeding colonies in the United States and a 67% survival rate for wild infants living beyond one year at Gombe. A more recent and expanded dataset collected from five wild chimpanzee populations, including Gombe, revealed that around 80% of infants survive past one year (Hill et al. 2001). Infants at Kanyawara experience a particularly high survival chance, at 89% (Muller & Wrangham 2014). Similar to what is observed in combined wild populations as well as in US colonies, 83% of live-born infants in Japan survived beyond one year of age, however this rate drops to 68% when non-live births are included. It is unclear whether all reports from the wild include stillbirths, however this is unlikely as such cases are difficult to observe and thus record.

Almost one in six chimpanzees in Japan are stillborn. Of 391 chimpanzees born from 1980 to 2016 in North American AZA-accredited zoos, 48 (12%) were stillborn (Saiyed et al. 2018). During the same time period, 63 of 415 (15%) infants in Japan were stillborn. From 1941 to 2000 at the Taronga Zoo in Australia, seven of 95 (7%) infants were stillborn and 18

individuals died on the same day of birth (Littleton 2005); in Japan, 45 of 344 (13%) chimpanzees were stillborn. These comparisons expose that chimpanzees experience a higher risk of being stillborn in Japan, however this may be in part due to the inclusion of miscarriages in stillbirth counts, which are not clearly defined in the database. While individuals born alive who did not survive until the second day of life were recorded as "live" birth, a few false stillbirth cases may exist (e.g. labelled "bite wound" or "already dead when found"). Contrary to our expectation that the captive stillbirth rate would decrease as rearing practices improved, it increased over the past decade. Further investigation is required to identify reasons for this.

In Japan, the average life expectancy of a live-born individual at birth is 28.3 years, whereas in the wild a chimpanzee is expected to live less than 15 years (Hill et al. 2001). However, this can depend on the environment of a population; some wild chimpanzees living under highly favorable conditions have an average life expectancy at birth of 32.8 years, higher than the captive population in Japan (Wood et al. 2017). Wild individuals who survive to adulthood (age 12) are likely to reach 30 years of age (Hill et al. 2001). Once a chimpanzee in Japan has reached their first birthday she or he is expected to live 33.6 more years, and after reaching adulthood (age 12) they are likely to reach 40.4 years of age, suggesting that a higher proportion of captive chimpanzees in Japan survive to old ages compared to their wild counterparts. Unlike wild populations where male mortality is significantly higher than females', survival curves for each sex in captivity in Japan do not differ significantly (Hill et al. 2001, Wood et al. 2017). For unknown reasons, females in Japan experience higher mortality than males in the first year of life, where only 78% of infants survive compared to 85% of males. At Taronga Zoo, 87% of females and 67% of males survived to one year; after this high risk period mortality levels were similar until adolescence, when males again experienced a higher risk

(Littleton 2005). Environment may shape mortality as much or more than phylogeny, so longevity differences are expected to be found across populations of same-species animals (Bronikowski et al. 2011). This appears to be the case for wild and captive chimpanzees.

The oldest chimpanzees living in wild populations are most commonly female and in their early 50s (Bronikowski et al. 2011, Matsuzawa et al. 2011). The oldest individual reported living in the wild is from the Ngogo community in Uganda, estimated to be 66 years old and one of five females above 60 (Wood et al. 2017). In AZA-accredited institutions in the US, data current to 2012 include the oldest chimpanzee ever documented, a wild-born female with an estimated life span of 74 years (+/- 4 y) at that time (Chimpanzee Species Survival Plan 2012). The oldest chimpanzee in the captive European population is a female estimated to have lived 60 years (Carlsen & de Jongh 2014). Unlike these captive and wild longevity records, the oldest individual in Japan was a male, estimated to be 68 years old (+/- 1 y). He is among one of the oldest documented chimpanzees in the world. The oldest female in Japan lived 59 years (+/- 1 y), nearly one decade less. While only five males in Japan surpassed or currently live past the age of 50, ten females do, suggesting that females reach older ages more frequently than males. This reflects maximum longevity patterns in the wild where the majority of old individuals are female.

To our knowledge, only one study has reported on whether wild chimpanzees experience different rates of mortality across seasons, but none have investigated this among captive living individuals. In the wild, a seasonal mortality pattern was not detected for the Gombe chimpanzee community as it was for other primate species, and periods of food scarcity did not significantly influence their death rate (Gogarten et al. 2012). In Japan, chimpanzees are more likely to pass away in one of the winter months (Dec—Feb) than during any other season. Although the causes

of heightened mortality during the winter season in Japan are unknown, it may be related to the constant cold temperatures which chimpanzees are not well adapted to. In captivity, food availability remains stable throughout the seasons and although indoor sleeping rooms are typically temperature controlled, it is not possible to carefully control outdoor conditions where most chimpanzees spend their day. Chimpanzees who are contained or choose to remain indoors might experience a heightened risk of injury, disease transmission and/or infection from humans. Other animals, including humans and dairy cows, also show an increased risk of mortality during periods of cold weather (Analitis et al. 2008; Cox et al. 2016).

The accuracy of infant survival rates, maximum longevity and life expectancy calculations depends partly on how long a captive population exists, therefore results are expected to vary over time. At establishment, a colony is not typically made up of individuals belonging to diverse age classes, but usually contains a majority of young animals. Thus, the presence of older individuals in a group is most likely a function of the age of the colony or institution where they are held (Dyke et al. 1995). Captive chimpanzees around the world are only recently developing into aging populations and so current life expectancy calculations are likely underestimated, until a larger number of individuals reach into old age and more data accrue (Faust et al. 2012b). Improved management and veterinarian practices over time may also influence these calculations. While we are able to show that the median age at death of chimpanzees in Japan is increasing year after year, we also illustrate how the age of individuals alive each year is increasing. This is necessary to take into consideration because chimpanzees in captivity have not yet reached their full aging potential; many were brought to Japan in the 1980's and thus current increasing lifespans may be an artefact of more old individuals existing. Whether or not life expectancy has increased over time due to improving practices in captivity is

a difficult question to answer and may require more time to pass before any meaningful conclusion is made (i.e. until the median age of those alive each year no longer increases). It should also be pointed out that due to the inclusion of early data (pre 1980's) in this study, a time when little was known about how to care for chimpanzees in captivity, life expectancy predictions for individuals living in Japan are likely to be underestimated.

Studbook and other historical databases are excellent resources for the study of animal biology, care and management (Fisken et al. 2018). Studbook data from accredited American zoos have previously been used to investigate chimpanzee birth timing (Wagner & Ross 2008) and great ape stillbirth rates (Saiyed et al. 2018), and from European zoos to understand chimpanzee geographic origins and admixture (Hvilsom et al. 2013). Few other databases exist such as AnAge (De Magalhães & Costa 2009), PanTHERIA (Jones et al. 2009) and All The World's Primates (Rowe & Myers 2017), but captive data are still most commonly maintained in difficult-to-access national or regional studbooks. The Great Ape Information Network is unique in that all available individual life history data on five ape species (all except humans) in Japan is recorded on a near daily basis and is openly accessible to interested researchers and the public. Future studies utilizing GAIN data will apply mortality estimates to investigate the relationship between longevity and reproductive parameters including age at first birth, inter-birth interval and number of offspring, and also between longevity and individual history of biomedical experimentation. As populations of chimpanzees and other long-lived animals in captivity around the world are steadily aging, it seems an appropriate time to analyze, or re-analyze, collated data in order to obtain a more complete understanding of their life history patterns.

2.5 Figures

Fig. 2.1 A chimpanzee eats a mango while another carefully observes at Kumamoto Sanctuary

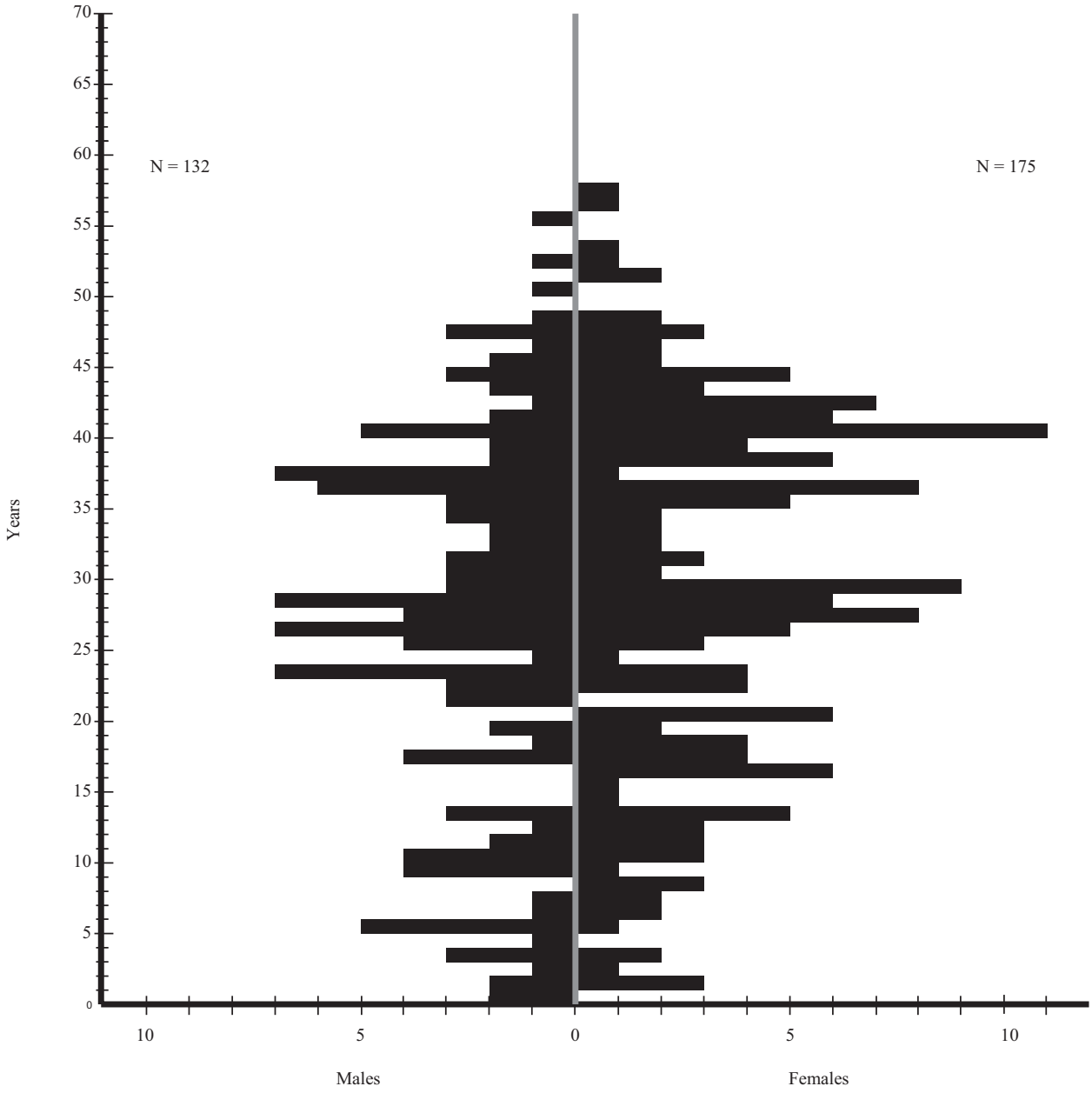

Fig. 2.2 Current age-sex composition of captive chimpanzees in Japan as of March 11, 2019 (n=307)

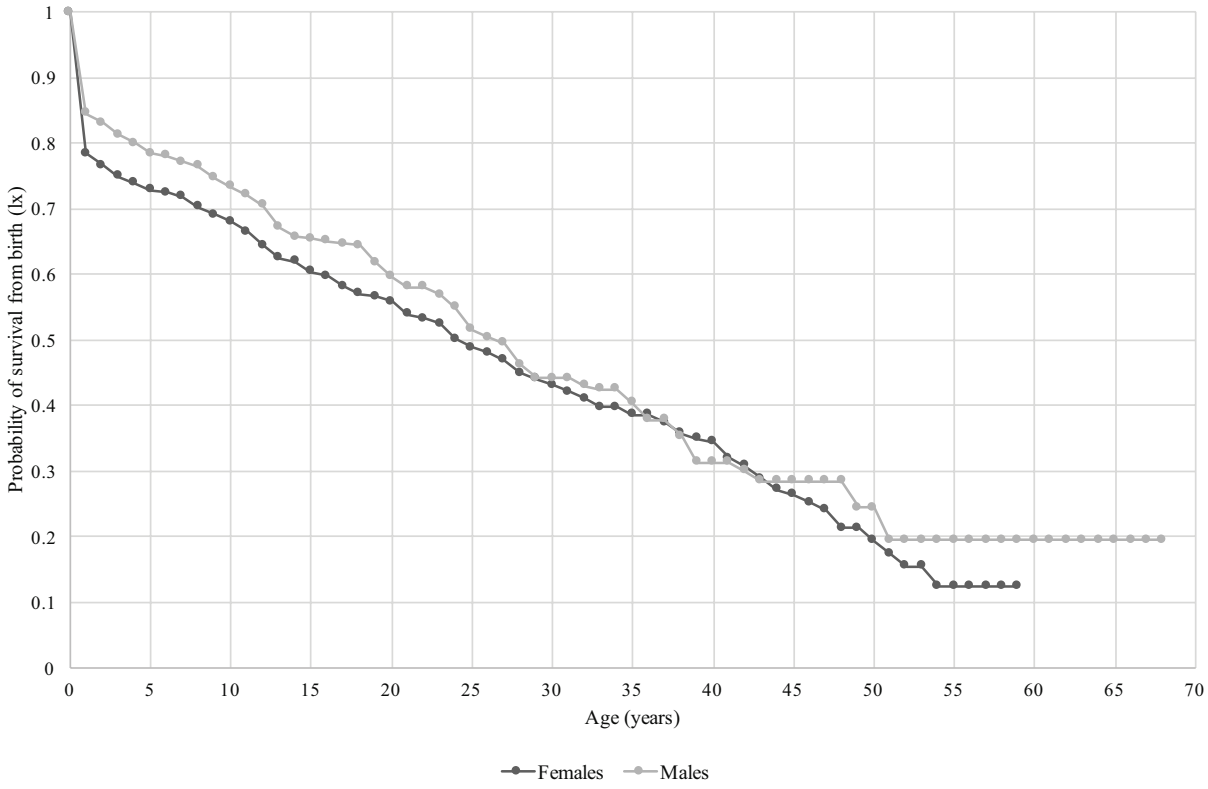

Fig. 2.3 Age-specific probability of survival from birth (l_x) for captive chimpanzees in Japan (n=821)

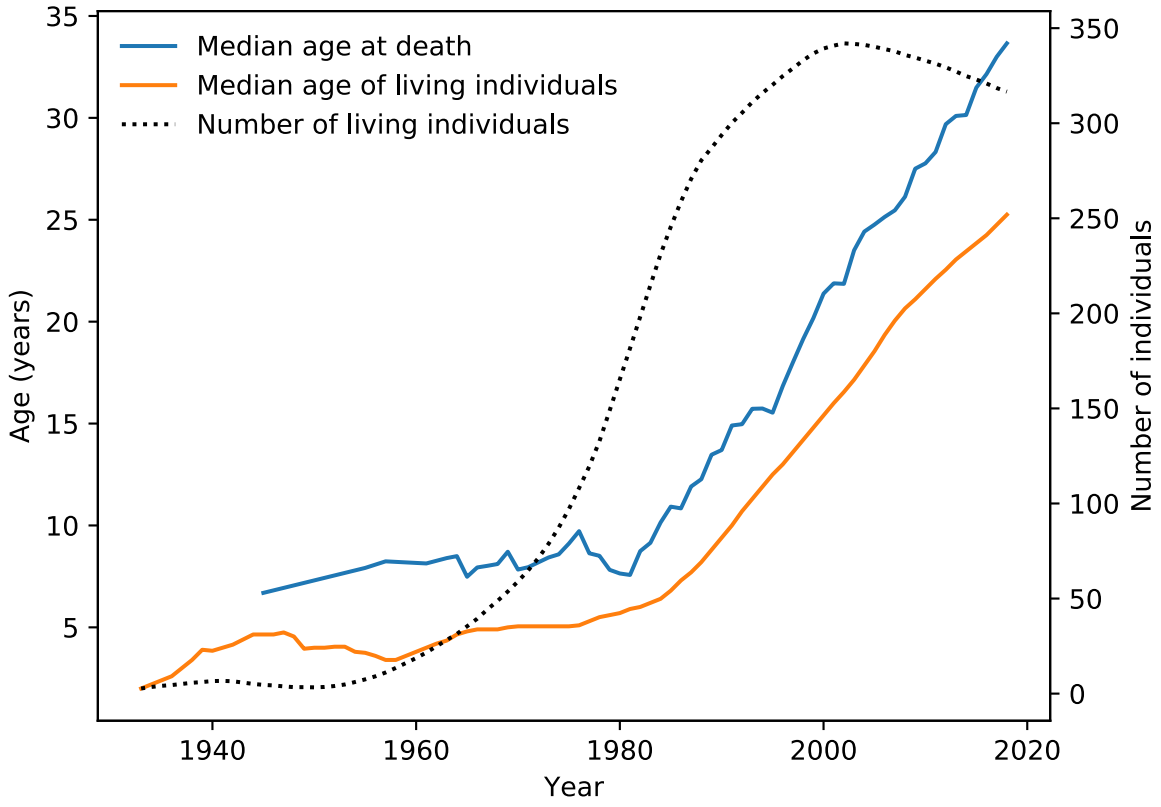

Fig. 2.4 Moving averages over ten years of the median age at death and of chimpanzees living each year in Japan

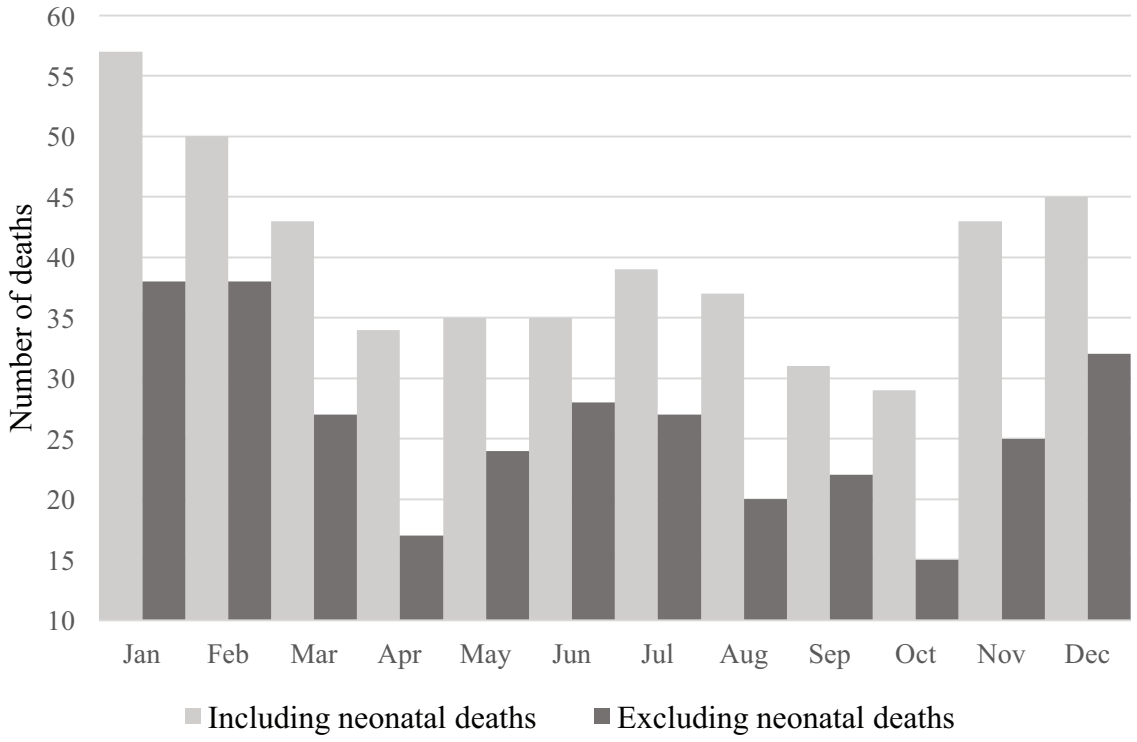

Fig. 2.5 Chimpanzee death rate by month in Japan (winter = Dec–Feb; spring = Mar–May; summer = Jun–Aug; Fall = Sep–Nov)

2.6 Tables

Table 2.1 Chimpanzee infant survival rates in Japan

	N	% incl. stillbirth	% incl. only live-born
Captive births (in Japan)	502		(N = 430)
Stillborn (non-live birth)	72	14.3%	-
Survival past one week	402	80.1%	93.5%
Survival past one year	341	67.9%	79.3%

Table 2.2a Ten oldest female chimpanzees in Japan

GAIN ID	Status	Origin	Estimated age at import (degree of error)	Age
7	Dead	Wild Born	1.7 y (+/-1)	59.1
11	Living	Unknown	2.0 y (+/-1)	57.6
15	Living	Unknown	1 m (+1)	56.9
2	Dead	Wild Born	1.9 y (+/-1)	53.5
26	Living	Wild Born	1.4 y (+/-1)	53.6
42	Living	Unknown	4.1 y (+/-1)	52.6
29	Living	Captive Born	n/a	51.6
81	Living	Unknown	7.9 y (+/-6m)	51.6
13	Dead	Captive Born	n/a	51.1
436	Dead	Wild Born	2.0 y (+/-2)	50.9

Table 2.2b Ten oldest male chimpanzees in Japan

GAIN ID	Status	Origin	Estimated age at import (degree of error)	Age
3	Dead	Wild Born	2.0 y (+/-2)	68.5
20	Living	Wild Born	1.0 y (+/-1)	55.6
437	Living	Wild Born	2.0 y (+/-2)	52.6
31	Dead	Unknown	1.7 y (+/-1)	50.5
33	Living	Captive Born	n/a	50.4
132	Living	Wild Born	6.3 y (+/-1)	48.6
1	Dead	Wild Born	6.9 y (+/-1)	48.1
126	Living	Unknown	2 y (+/-2)	47.6
110	Living	Wild Born	4.7 y (+/-1)	47.6
72	Living	Wild Born	1.5 y (+/-1m)	46.9

Table 2.3 Life table by single year of age and sex for captive chimpanzees in Japan spanning 1921 to February 2019 (n=821).

n_x = Number of individuals at risk; d_x = number of deaths between age x and x + 1; q_x = probability of death within age interval (x, x + n); l_x (0y) = probability of survival from birth to age x; l_x (1y) = probability of survival from 1 year to age x; l_x (5y) = probability of survival from 5 years to age x; e_x = remaining life expectancy (years) at age x.

	Females							**Males**						
Age	n_x	d_x	q_x	l_x (0y)	l_x (1y)	l_x (5y)	e_x	n_x	d_x	q_x	l_x (0y)	l_x (1y)	l_x (5y)	e_x
0	222	48	0.22	1.00			26.3	194	30	0.15	1.00			30.3
1	212	5	0.02	0.78	1.00		32.4	181	3	0.02	0.85	1.00		34.7
2	289	6	0.02	0.77	0.98		32.2	223	5	0.02	0.83	0.98		34.3
3	334	5	0.01	0.75	0.96		31.8	248	4	0.02	0.81	0.96		34.1
4	352	5	0.01	0.74	0.94		31.3	251	5	0.02	0.80	0.95		33.6
5	363	2	0.01	0.73	0.93	1.00	30.8	256	1	0.00	0.78	0.93	1.00	33.3
6	364	3	0.01	0.72	0.92	0.99	29.9	251	3	0.01	0.78	0.92	1.00	32.4
7	364	8	0.02	0.72	0.92	0.99	29.2	248	2	0.01	0.77	0.91	0.98	31.8
8	355	6	0.02	0.70	0.90	0.96	28.8	245	6	0.02	0.77	0.91	0.98	31.1
9	347	5	0.01	0.69	0.88	0.95	28.3	239	4	0.02	0.75	0.88	0.95	30.8
10	338	8	0.02	0.68	0.87	0.93	27.7	230	4	0.02	0.73	0.87	0.94	30.3
11	325	10	0.03	0.66	0.85	0.91	27.4	219	5	0.02	0.72	0.85	0.92	29.9
12	310	9	0.03	0.64	0.82	0.88	27.2	209	10	0.05	0.70	0.83	0.90	29.5

13	297	3	0.01	0.62	0.80	0.86	27.0	199	4	0.02	0.67	0.79	0.86	30.0
14	288	7	0.02	0.62	0.79	0.85	26.3	186	1	0.01	0.66	0.78	0.84	29.6
15	276	3	0.01	0.60	0.77	0.83	25.9	187	1	0.01	0.65	0.77	0.83	28.8
16	271	7	0.03	0.60	0.76	0.82	25.2	183	1	0.01	0.65	0.77	0.83	27.9
17	258	5	0.02	0.58	0.74	0.80	24.9	181	1	0.01	0.65	0.77	0.83	27.1
18	245	2	0.01	0.57	0.73	0.78	24.3	176	7	0.04	0.64	0.76	0.82	26.2
19	237	3	0.01	0.57	0.72	0.78	23.5	167	6	0.04	0.62	0.73	0.79	26.3
20	232	8	0.03	0.56	0.71	0.77	22.8	159	4	0.03	0.60	0.70	0.76	26.2
21	217	3	0.01	0.54	0.69	0.74	22.6	153	0	0.00	0.58	0.69	0.74	25.9
22	212	3	0.01	0.53	0.68	0.73	21.9	151	3	0.02	0.58	0.69	0.74	24.9
23	206	9	0.04	0.52	0.67	0.72	21.3	144	5	0.03	0.57	0.67	0.73	24.4
24	191	5	0.03	0.50	0.64	0.69	21.2	132	8	0.06	0.55	0.65	0.70	24.3
25	183	3	0.02	0.49	0.62	0.67	20.8	122	3	0.02	0.52	0.61	0.66	24.8
26	176	4	0.02	0.48	0.61	0.66	20.1	115	2	0.02	0.50	0.60	0.64	24.4
27	165	7	0.04	0.47	0.60	0.64	19.5	107	7	0.07	0.49	0.58	0.63	23.8
28	152	3	0.02	0.45	0.57	0.62	19.4	92	4	0.04	0.46	0.55	0.59	24.5
29	142	3	0.02	0.44	0.56	0.61	18.8	81	0	0.00	0.44	0.52	0.56	24.6
30	129	3	0.02	0.43	0.55	0.59	18.2	78	0	0.00	0.44	0.52	0.56	23.6
31	123	3	0.02	0.42	0.54	0.58	17.6	75	2	0.03	0.44	0.52	0.56	22.6
32	117	4	0.03	0.41	0.52	0.56	17.0	70	1	0.01	0.43	0.51	0.55	22.2
33	111	0	0.00	0.40	0.51	0.55	16.6	67	0	0.00	0.42	0.50	0.54	21.5
34	109	3	0.03	0.40	0.51	0.55	15.6	65	3	0.05	0.42	0.50	0.54	20.5
35	104	0	0.00	0.39	0.49	0.53	15.0	60	4	0.07	0.40	0.48	0.52	20.4
36	100	3	0.03	0.39	0.49	0.53	14.0	52	0	0.00	0.38	0.45	0.48	20.9
37	90	4	0.04	0.37	0.48	0.51	13.4	46	3	0.07	0.38	0.45	0.48	19.9
38	83	2	0.02	0.36	0.46	0.49	13.0	36	4	0.11	0.35	0.42	0.45	20.2
39	76	1	0.01	0.35	0.45	0.48	12.4	30	0	0.00	0.31	0.37	0.40	21.7
40	70	5	0.07	0.34	0.44	0.47	11.5	28	0	0.00	0.31	0.37	0.40	20.7
41	54	2	0.04	0.32	0.41	0.44	11.4	23	1	0.04	0.31	0.37	0.40	19.7

42	46	3	0.07	0.31	0.39	0.42	10.8	20	1	0.05	0.30	0.35	0.38	19.6
43	36	2	0.06	0.29	0.37	0.40	10.5	18	0	0.00	0.29	0.34	0.36	19.6
44	31	1	0.03	0.27	0.35	0.37	10.1	16	0	0.00	0.29	0.34	0.36	18.6
45	24	1	0.04	0.26	0.34	0.36	9.4	13	0	0.00	0.29	0.34	0.36	17.6
46	21	1	0.05	0.25	0.32	0.35	8.8	11	0	0.00	0.29	0.34	0.36	16.6
47	18	2	0.11	0.24	0.31	0.33	8.2	10	0	0.00	0.29	0.34	0.36	15.6
48	14	0	0.00	0.21	0.27	0.29	8.2	7	1	0.14	0.29	0.34	0.36	14.6
49	11	1	0.09	0.21	0.27	0.29	7.2	5	0	0.00	0.24	0.29	0.31	15.9
50	10	1	0.10	0.19	0.25	0.27	6.8	5	1	0.20	0.24	0.29	0.31	14.9
51	9	1	0.11	0.17	0.22	0.24	6.5	3	0	0.00	0.20	0.23	0.25	17.5
52	6	0	0.00	0.16	0.20	0.21	6.3	3	0	0.00	0.20	0.23	0.25	16.5
53	5	1	0.20	0.16	0.20	0.21	5.3	2	0	0.00	0.20	0.23	0.25	15.5
54	3	0	0.00	0.12	0.16	0.17	5.5	2	0	0.00	0.20	0.23	0.25	14.5
55	3	0	0.00	0.12	0.16	0.17	4.5	2	0	0.00	0.20	0.23	0.25	13.5
56	3	0	0.00	0.12	0.16	0.17	3.5	1	0	0.00	0.20	0.23	0.25	12.5
57	3	0	0.00	0.12	0.16	0.17	2.5	1	0	0.00	0.20	0.23	0.25	11.5
58	1	0	0.00	0.12	0.16	0.17	1.5	1	0	0.00	0.20	0.23	0.25	10.5
59	1	1	1.00	0.12	0.16	0.17	0.5	1	0	0.00	0.20	0.23	0.25	9.5
60								1	0	0.00	0.20	0.23	0.25	8.5
61								1	0	0.00	0.20	0.23	0.25	7.5
62								1	0	0.00	0.20	0.23	0.25	6.5
63								1	0	0.00	0.20	0.23	0.25	5.5
64								1	0	0.00	0.20	0.23	0.25	4.5
65								1	0	0.00	0.20	0.23	0.25	3.5
66								1	0	0.00	0.20	0.23	0.25	2.5
67								1	0	0.00	0.20	0.23	0.25	1.5
68								1	1	1.00	0.20	0.23	0.25	0.5

Chapter 3

Comparative survival analyses among captive chimpanzees (*Pan troglodytes*) in America and Japan

3.1 Introduction

Studying life history patterns of non-human primates is important for understanding the evolution of human life histories and senescence (Bronikowski et al., 2011). In particular, chimpanzee survival and mortality patterns have been studied to explore differences with other species, among populations of chimpanzees in the wild, and between wild and captive populations (e.g. Earnhardt et al., 2003; Hill et al., 2001; Thompson et al., 2007; Muller & Wrangham, 2014; Tidière et al., 2016; Wood et al., 2017; Davison & Gurven, 2021). Detailed, long-term datasets on life histories are rare but important for capturing survival rates at later ages, especially for long-lived species such as chimpanzees. Comparing chimpanzee survival across different captive populations may expose similarities or differences in survival patterns which could be further examined for determining best management strategies such as husbandry techniques, diet and veterinary care.

Chimpanzees are one of humans' closest living relatives and have been studied for decades, which has allowed for the comparison of life history patterns to shed light on human evolution (e.g. Hawkes, Smith & Robson, 2009; Hill et al., 2001; Muller & Wrangham, 2014; Thompson et al., 2007; Wood et al., 2017; Davison & Gurven, 2021). Life expectancy at birth for hunter-gatherers ranges from 21-37 years across groups and between 26-43% of people survive to age 45 (Gurven & Kaplan, 2007), similar to what has been found in a wild (Wood et al., 2017) and a captive chimpanzee population (Havercamp et al., 2019). The average life

expectancy of wild chimpanzees varies across populations (Table 3.1). Data from five sites across Africa show that individuals who survive to adulthood (14 y) have a life expectancy of approximately 29 years (Hill et al., 2001). In Kanyawara in East Africa, adult chimpanzees (14 y) can expect to live 38 years (Muller & Wrangham, 2014) and at Ngogo, also in East Africa, 43 years (Wood et al., 2017). In captivity in Japan, a 14-year old individual is expected to reach 42 years of age (Havercamp et al., 2019). Longevity estimates of chimpanzees from birth are lower due to the high risk infant period, from 13 years across five sites (Hill et al., 2001), 19 years at Kanyawara (Muller & Wrangham, 2014), 28 years in captivity (Havercamp et al., 2019), to 33 years at Ngogo (Wood et al., 2017). Typically, mammals live longer in captive environments such as zoos compared to in the wild, although some long-lived species such as elephants and chimpanzees do not (Tidière et al., 2016).

There are several existing reports on captive chimpanzee survival which serve to inform our understanding of life histories (Table 3.1). Unfortunately, they are now outdated, derived from relatively small samples or missing data on older individuals. Courtenay & Santow (1989) published the first life table, though it was derived from just 87 individuals and mortality estimates were only calculated up to age 30 due to the short history of the population at that time. Dyke et al. (1995) presented modelled data including 1,488 individuals from three colonies in America and reported that males and females had an expected lifespan of 21 years and 29 years respectively when calculated from birth. When calculated from adulthood (14 years), males had an expected lifespan of 33 years and females 41 years. However, because the modelled life tables represented an average of various sources of variability, they urged caution in using these data as a representation of chimpanzees. In a later study, chimpanzees at Taronga Park Zoo in Australia experienced higher mortality risk from birth than wild chimpanzees in Mahale or Gombe. They

also reported that females had greater life expectancy than males, however the size of the captive population was only 113 and the life table reached only 51 years of age (Littleton, 2005).

Historically, America and Japan have held the largest number of captive chimpanzees in the world, over 3000 individuals combined, and the trajectory of those populations have been described in detail by Hirata et al. (2020). The earliest record of a chimpanzee in America is from 1902, whereas the first chimpanzee arrived in Japan around two decades later, in 1921. America adopted the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1975, ceasing the importation of chimpanzees captured in Africa. Japan followed soon after ratifying CITES in 1980, however was still able to import wild chimpanzees under special circumstances for research until 1983. Broadly speaking, the populations are relatively similar in terms of their management at an individual and group level, however there are likely some differences at the population level. While the Japan population is largely self-contained and its growth is dependent on births in zoos, the America population has a significant proportion of chimpanzees that have entered the population from external sources such as research centers, the entertainment industry, and the pet trade (Hirata et al., 2020).

We synthesize data from these two regional captive populations to yield the largest dataset on chimpanzee life history and report the first systematic comparison of survival patterns for a primate species across regions. We present life tables by age and sex and statistics for chimpanzee survival and life expectancy for both the America population living in zoos accredited by the Association of Zoos and Aquariums (AZA) and the Japan population living in zoos and one sanctuary. We use studbook records, covering the modern history of these apes in each country to examine whether differences in longevity and survival exist between the two populations over a comparable time period. We hypothesized that the two populations would

show similar life history patterns for survivorship and longevity, and demonstrate similar influences of sex and birth type (wild or captive born) on these variables. We did not have a priori predictions on how the survival patterns may differ between regions based on our knowledge of the welfare and management of the two populations. Factors contributing to survival rates such as diet, the ways and levels of veterinary care, and the specific physical and social environments differ between regions but also vary greatly between facilities within each region. Thus there is unlikely to be a consistent difference between countries that would impact survival metrics at the regional scale. We also predicted that survivorship for both populations would increase in the more recent timeframe (2001-2020) and tested whether mortality varied by season in the AZA population as was shown in the Japan population (Havercamp et al. 2019). Such cross-region population comparisons may help elucidate potential life history outcomes affected by differences in captive care and management.

3.2 Materials & Methods

3.2.1 Data collection

We accessed demographic data for the chimpanzee population housed in AZA accredited facilities via the North American Regional Studbook for Chimpanzees (Ross, 2020), the most robust and consistent record of chimpanzees in the United States. Over more than a century, thousands of chimpanzees have lived in a range of captive settings in America including laboratories, zoos (accredited and unaccredited), sanctuaries (accredited and unaccredited), and in private hands (as pets or performers). Due to the varied nature of housing facilities and the historically loose regulation of cross-facility transfers, there was no comprehensive record of the U.S.-based chimpanzee population until Lincoln Park Zoo's Project ChimpCARE, founded in

2007, began censusing all chimpanzees in the country (www.chimpcare.org). The North American Regional Studbook (Ross, 2020) contains records of 1302 chimpanzees since 1902, most of whom have lived in accredited zoos. At the time of writing, 260 chimpanzees lived in 31 AZA-accredited facilities in the United States, whereas Project ChimpCARE estimates that 1382 were alive across all settings (including zoos, sanctuaries, private owners, laboratories, and unaccredited facilities).

Similarly, we accessed data on captive chimpanzees living in zoos and a sanctuary in Japan via the open-access Great Ape Information Network (GAIN; https://shigen.nig.ac.jp/gain/; Havercamp et al., 2019) using PopLink software (Faust et al., 2019). Chimpanzees in Japan have been tracked via GAIN since the program was initiated in 2002 (Matsuzawa, 2016; Ochiai et al., 2015; Watanuki et al., 2014). The database has been utilized for a recent demographic analysis of this population (Havercamp et al., 2019). There are records for 1025 (possibly 1067) individuals who have lived in Japan since 1921, most of whom were housed in zoos, but also in eight biomedical research institutions, universities, and a sanctuary. In total, 205 were subjects of biomedical research (Hirata et al., 2020). At the time of writing, 302 chimpanzees live across 48 facilities including 46 zoos, animal or amusement parks, one university institute (12 individuals; Primate Research Institute of Kyoto University), and one sanctuary (50 individuals; Kumamoto Sanctuary of Kyoto University established in 2011, which was a former biomedical institution before it was reformed into Chimpanzee Sanctuary Uto in 2007; Morimura et al., 2011).

For both populations, we included for analysis individuals with a known birth location who had at least a portion of their lifespan within a time frame that reflected modern population management (1/1/1975 to 2/1/2020 for AZA, 1/1/1980 to 2/1/2020 for Japan). We selected these ranges based on the years when America and Japan ratified CITES. For the AZA population, we

also filtered to include the portion of lifespans that occurred within AZA-accredited facilities. We did not include records for chimpanzees who do not live in accredited zoo settings (i.e., laboratory, private, sanctuary). Some individuals had uncertainty in their birth dates, and our results should be interpreted with these in mind. Of the 730 total individuals (320 males, 389 females, and 21 individuals of unknown sex) across 94 facilities included from the AZA population, 563 had known birthdates. The remaining had a recorded birth date plus a time window reflecting the recorder's uncertainty in the actual birth date (e.g., Jan. 1, 1993 ± one month): three individuals had estimates that were within four years of the actual birth date, 104 within two years, 28 within one year, one within six months, and 31 within one month. Of the 660 total individuals (292 males, 364 females, 4 individuals of unknown sex) across 77 facilities included from the Japan population, 486 had known birth dates, while 172 had birth date estimates that were within one year and two had estimates within one month of the actual birthdate. Finally, we excluded miscarriage and stillbirth events in the studbook (records of individuals who died on their birthdates), of which there were 59 in AZA and 50 in Japan.

3.2.2 Life tables

Using these data, we calculated life tables for each population using PMx software (Ballou, Lacy & Pollak, 2020), consisting of Kaplan–Meier estimates of annual age-specific mortality (q_x) and fecundity (M_x) rates (Lacy, Ballou & Pollak, 2012). We included individuals of unknown sex, all of whom died (4 individuals in Japan and 19 in AZA) or were lost to follow-up (2 in AZA) within their first year of life, in the life table calculations to more accurately reflect the observed rate of first-year mortality. They were distributed as 0.5 male and 0.5 female following the standard in PMx (indivdiuals of unknown sex were excluded from all remaining

analyses). To compare against a recently published life table for a wild chimpanzee population in Gombe, Tanzania (Bronikowski et al., 2016), we calculated l_x (survival to age x) using q_x (probability of death within a year for age x individuals) from our PMx life tables as: $l_x = l_{x-1}*(1-q_{x-1})$, and $l_o = 1.0$.

3.2.3 Survival patterns and population comparisons

We conducted survival analyses (Kleinbaum & Klein, 2005) using the *survival* R package (Therneau, 2021) to describe the survival patterns in each population and to test for differences between the two populations. First, we used Cox proportional hazards regression to test whether survival curves differed by sex, birth type (wild-born or captive-born), and their interaction for each population separately. After excluding individuals of unknown sex, there were 69 wild-born males, 251 captive-born males, 100 wild-born females, and 289 captive-born females in the AZA population. For the Japan population, there were 62 wild-born males, 230 captive-born males, 105 wild-born females, and 259 captive-born females. We then combined the data for both populations and tested whether survival curves differed by sex, birth type, region (AZA or Japan), and all possible interactions. We removed any non-significant ($p>0.05$, but all had $p>0.1$) interaction terms in the final models. We also used the Kaplan-Meier method to fit observed survival curves based on the significant predictors, and to estimate the median life expectancy for each population by sex. We performed survival analyses starting at birth and starting at age one to assess whether patterns change when neonatal mortality was excluded.

3.2.4 Distribution of age at death by population

We next examined longevity over time in each population. We first calculated the age at mortality for each observed death event and divided the events into two time periods ("early" = 1975-2000 for AZA and 1980-2000 for Japan, "recent" = 2001-2020 for both). In total, there were 197 deaths observed in the early period and 150 in the recent period for the AZA population, and 139 deaths observed in the early period and 168 in the recent period for the Japan population. We then used Poisson regression to test whether the mean age at mortality differed based on sex, birth type, and between the two time periods. That is, we modeled the observed ages at mortality as a Poisson-distributed response variable in a generalized linear model with a log link function to analyze the effects of sex, birth type, and time period on the mean age at death. We used the function *glm* in the *stats* R package (R Core Team, 2020), and specified the quasipoisson family to account for overdispersion in the response. Because no deaths before age one were observed in wild born individuals, we conducted the analysis using only mortalities that occurred on or after the first birthday.

3.2.5 Seasonal death patterns

Finally, we assessed seasonal patterns in mortality for the AZA population, replicating an analysis previously conducted for the Japan population (Havercamp et al., 2019). For this, we tallied the number of observed deaths by season (spring = March through May, summer = June through August, autumn = September through November, winter = December through February). We applied a Chi-square goodness of fit test (using function *chisq.test* in the *stats* R package [R Core Team, 2020]) to compare the observed proportion of mortality in each season to the expected proportion (25% each, or evenly distributed across seasons). We also analyzed only mortalities that occurred on or after the first birthday, and re-analyzed data from the Japan

population to match the time frame used in this study (1980-2020). Except where specified, all survival and statistical analyses were performed in R (R Core Team, 2020) and statistical significance was determined using the criterion $p \leq 0.05$.

3.3 Results

3.3.1 Life tables

We present the full life table for the AZA population and Japan population (Tables 3.S1 and 3.S2, respectively; Fig. 3.1). The longest observed lifespan was longer in the AZA population, with one female surviving to an estimated age of 79, whereas one male survived to estimated age 68 in the Japan population. The longest-lived captive-born (confirmed age) individual in AZA was 57 and in Japan is 53 (still alive). First year mortality was significantly lower in AZA (15%) than Japan (25%; $z = -2.3$, $p = 0.02$) for females, and similar between AZA (18%) and Japan (20%) for males ($z = -0.6$, $p = 0.58$). Comparing the survival curves for our two captive populations against that for a wild population from Tanzania, we found that captive chimpanzees experienced a higher survival probability than wild chimpanzees starting at age 2 (Fig. 3.1).

3.3.2 Survival patterns and population comparisons

When analyzing each population separately, we found survival patterns differed by sex but not birth type in the AZA population. AZA males had higher overall mortality rates than AZA females, both when examining survival from birth (coefficient = 0.41, $z = 2.7$, $P < 0.01$) and from age one (coefficient = 0.51, $z = 2.8$, $P < 0.01$). Survival patterns did not differ by sex or birth type in the Japan population ($P > 0.15$ in all cases). Accordingly, median life expectancy estimates from birth are lower for males than females in AZA (28.4 years and 36.7 years,

respectively) but similar between sexes in Japan (34.0 years and 34.1 years, respectively; Table 3.2). From age one, a similar difference in median life expectancy exists between the sexes in AZA (32.5 years for males, 41.9 years for females), and a slight difference appears in Japan (37.7 years for males, 42.4 years for females; Table 3.2).

When combining data from both populations to compare survival patterns between regions, the results differed slightly depending on whether we included or excluded neonatal mortality (Fig. 3.S1). Survival patterns from birth showed a significant effect of sex (coefficient = 0.39, z = 3.2, $P < 0.01$) and an interaction between region and sex (coefficient = -0.39, z = -2.3, $P = 0.02$): males have lower survival than females overall, but the difference is larger in AZA than Japan. Survival from age one showed an effect of sex (coefficient = 0.31, z = 3.0, $P < 0.01$), again with higher mortality for males. The Japan population had slightly lower mortality rates than the AZA population, but the difference was not significant (coefficient = -0.19, z = -1.8, $P = 0.07$; Fig. 3.S1) and there were no significant interactions among predictors.

3.3.3 Distribution of age at death by population

Comparing longevity over time also showed slight differences between populations, with interacting effects of sex, birth type, and time period on age at death for both populations (Table 3.3; Fig. 3.2). Although we did not analyze deaths before age one in this analysis, we note that more neonatal deaths occurred before 2001 than since 2001 in captive-born individuals; neonatal deaths were not possible to observe in wild born individuals. For the AZA population, 43 of 141 observed deaths (30%) in the early time frame occurred before the first birthday, compared to 15 of 139 (11%) deaths observed in the recent time frame having occurred before age one. For the

Japan population, 45 of 111 deaths (41%) in the early time frame occurred before the first birthday, compared to 43 of 146 deaths (29%) in the recent time frame.

For the AZA population, the mean ages at death differed by time period and birth type but not by sex (Table 3.3), with mortality on average occurring later for wild born individuals and in the recent time frame (Fig. 3.2A). The two-way interaction between time period and birth type was also significant (Table 3.3), with a slightly larger difference in age at death between captive and wild born individuals in the later time frame compared to the earlier time frame (Fig. 3.2). When focusing specifically on the early time period for the AZA population, we found the median age of death was very similar for wild-born males and females (F=26.4, M=27.8) and lower for captive-born individuals (F=11.1, M=10.3). Considering only the more recent time frame, the mean age at death was higher for both wild-born (F=47.0, M=42.0) and captive born (F=27.1, M=21.3) chimpanzees. It is important to note that the population was younger overall in the early time period: the mean age of the AZA population was only 14.5 in the early time period (averaged across years within the time frame), and 23.7 in the recent time period (see Fig. 3.3 for mean age of the population in each year).

For the Japan population, the mean ages at death differed by all predictors (Table 3.3), and the three-way interaction as well as the two-way interaction between sex and birth type were also significant (Table 3.3). The three-way interaction meant that, for example, the difference in age at death between males and females depended on both the time period and birth type. Captive born females died at a younger age than captive born males, but wild born females survived to an older age than wild born males, and this was more apparent in the early time period. The estimated mean age at death in the early time period was 22.9 and 17.5 for wild born females and males, respectively, and 11.3 and 17.8 for captive females and males, respectively.

In the recent time period, the estimated mean age at death was 38.7 and 38.4 for wild born females and males, respectively, and 22.2 and 22.9 for captive females and males, respectively. For context, the mean age of the Japan population was 11.1 in the early time period and 22.2 in the recent time period (Fig. 3.3).

3.3.4 Seasonal death patterns

In examining seasonal patterns of mortality, we confirmed previously published findings (Havercamp et al. 2019) that deaths in the Japan population were not evenly distributed across seasons. To compare to these earlier reports, we used only data since 1980 and found a significant deviation from the expectation of even distribution both when considering all deaths ($\chi^2 = 13.77$, df = 3, P < 0.01) and when excluding neonatal mortality ($\chi^2 = 11.95$, df = 3, P < 0.01), with the largest proportion of deaths occurring in winter. We did not find such a seasonal pattern in the AZA population, both in analysis of all deaths ($\chi^2 = 6.37$, df = 3, $P = 0.09$) and when considering only deaths after age one ($\chi^2 = 4.20$, df = 3, $P = 0.24$; Fig. 3.4).

3.4 Discussion

Although there are several published reports on life histories of captive chimpanzee populations (Courtenay & Santow, 1989; Dyke et al., 1995; Littleton, 2005; Havercamp et al., 2019), we believe this is the first to compare the life histories of two large captive chimpanzee populations from different regions. Such a comparative approach provides additional insights that may inform managers about the life history characteristics that are more (or less) flexible or potentially affected by different management practices.

Both of these populations of chimpanzees have been evaluated in previous studies, but the current datasets differ from previous ones in some important ways, primarily to facilitate cross-region comparisons. Earnhardt et al. (2003) used data from the AZA studbook to compare life histories of these chimpanzees to wild chimpanzees living at Gombe Stream National Park in Tanzania. That dataset represented 524 zoo-housed chimpanzees living from 1963 to 2003, compared to 730 from 1975 to 2020 in the current analysis. Likewise, an earlier study (Havercamp et al., 2019) analyzed the historical chimpanzee population living in Japan, using data for 821 chimpanzees from 1921 to 2018 compared to 660 from 1980 to 2020. For both populations, the current analysis represents a more narrow and more recent time frame, and the median life expectancies from the previous analyses were lower than those derived from this study, especially for females. This may be attributed in part to the more recent time frame reflecting more modern management practices that positively influence life history outcomes for these managed populations. For the AZA population, the earlier analysis (Earnhardt et al., 2003) included data up to 2003 and thus the younger population at that time (Fig. 3.3) could have also contributed to the shorter life expectancy estimates. However, the earlier analysis of the Japan population (Havercamp et al., 2019) included data through 2018 so the difference in our analysis is mainly excluding the earlier records, and thus are more likely to reflect recent refinements in management.

Combined, the dataset used here represents the lives of 1390 chimpanzees living in accredited zoos in America and zoos and a sanctuary in Japan. Using data from birth, median life expectancy (MLE) is 35.7 for females and 30.1 for males (Table 3.2), which is higher than most longevity estimates for wild chimpanzees. Hill et al. (2001) reported an MLE of just 13 years from data collected at five sites across Africa (see Table 3.1), and Muller & Wrangham (2014)

reported an MLE of 19 years at Kanyawara, Uganda. However, recent data from Ngogo, Uganda placed life expectancy at over 33 years for that population (Wood et al., 2017). In a direct comparison of wild and captive chimpanzee survivorship, Earnhardt et al. (2003) found that chimpanzees from AZA zoos typically lived longer than those living in Gombe Stream National Park in Tanzania. In comparing the survival curves of our two captive populations with a wild chimpanzee population living in Tanzania (Bronikowski et al., 2016; Fig. 3.1), we also found support for this pattern; at almost all ages from birth and from one year of age, captive chimpanzees experienced a higher survival probability. Interestingly, although Tidière et al. (2016) showed that mammals generally live longer in captive environments such as zoos compared to in the wild, they found the opposite trend for chimpanzees specifically. Moreover, survival statistics can vary greatly across wild populations (Davison & Gurven, 2021), so our comparison does not represent all wild populations (i.e., see Wood et al. 2017 for a population with higher survivorship). While these comparisons are worthwhile, we must acknowledge that survivorship comparisons are complicated because of the difficulty in assessing early life mortality for wild chimpanzees, including stillbirths. We removed stillbirths from these analyses, but it is impossible to say how stillbirth rates in captive settings, documented at 12% for AZA (Saiyed et al., 2018) and 15% for Japan (Havercamp et al., 2019), compare to those experienced by wild-living chimpanzees.

One of the most robust findings in this analysis was the sex difference in mortality demonstrated in the AZA chimpanzee population. Whether calculated from birth or after the age of one, males had higher mortality rates and shorter life expectancies when compared to females in the same managed population. Such sex differences are reflected by findings from a number of wild chimpanzee populations (Hill et al., 2001; Muller & Wrangham, 2014; Wood et al., 2017)

as well as other mammals (Tidière et al., 2016) and are broadly consistent with sexual selection theory. For many species, including chimpanzees, males are perceived as engaging in more risky behaviors (for instance, hunting and intergroup aggression) which increase the mortality risk. The human literature also reports female advantages in life expectancy that could be tied to a range of genetic, hormonal, metabolic, immune function and other biological factors (Seifarth et al., 2012). For instance, Vina et al. (2011) showed that the higher levels of estrogens in human females buffer them against the negative effects of aging, by up-regulating the expression of antioxidant and longevity-related genes.

Interestingly, such sex differences were not evident in the Japanese population and may be explained in part by regional differences in early life histories. Female first-year mortality in Japan was significantly higher than in AZA, suggesting that challenges in birth management and early life care may contribute to increased female mortality rates and a narrowing of the sex gap in mortality one might expect. Comparing the two regions, while female survival seems similar for females in both regions, males in the AZA population have lower survival than males in the Japan population. Explanations for these differences are unclear to us at this time. Though housing conditions and group compositions are not recorded as part of these datasets, we know anecdotally that in general, chimpanzee groups in AZA are larger than those in Japanese zoos and are more likely to have a multimale composition. Historically, some have speculated that males living with fewer or no other males may be under lower daily stress (Alford et al., 1995; Williams et al., 2010), but recent studies contradict this idea and demonstrate that males can live together in mixed-sex or multi-male groups without experiencing heightened aggression or stress levels (Neal Webb, Hau & Schapiro, 2019; Ross et al., 2009; Seres, Aureli & de Waal, 2001; Yamanashi et al., 2016). In a multi-institutional study of AZA-accredited zoos, multi-male

groups showed lower rates of wounding than single male groups (Ross et al., 2009). Likewise, an all-male group did not show heightened hair cortisol (HC) concentration (a proxy for stress), whereas the alpha male in a mixed-sex group showed the highest level of HC and aggression (Yamanashi et al., 2016). Nonetheless, the effect of social group composition on health and stress levels is not clear, and so whether this may create a difference in male survival between the two regions is unknown. Other potential factors, such as diet differences in the two regions, may be particularly ripe for future study and we encourage further refinement and extension of cross-regional comparisons of life histories for chimpanzees and other species under intense population management.

In addition to sex effects on life expectancy, we examined the effects of whether chimpanzees were born in the wild or born in captivity. Overall survival patterns did not differ for those born in captive settings compared to those born in the wild, for either the AZA or the Japan population. However, differences in age at death between sexes depended on birth type. In the AZA population, males died younger than females, but this sex difference was smaller for wild-born versus captive born individuals. In Japan, captive-born males tended to die later than captive-born females, but wild-born males died younger than wild-born females. These analyses of birth origin need to be interpreted in context of the fact that early life histories of wild-born individuals are not available (i.e. there are fewer observed deaths in the younger ages, before transfer into captive populations). Also, many wild-born individuals who were captured may not have survived the travails of capture and transport and are therefore not represented in these analyses. This may be an example of the related concepts of selective disappearance and mortality selection (Vaupel et al., 1979; Vaupel & Yashin, 1985; Hämäläinen et al., 2014) in which the capture process could have selected for healthier individuals who would thus have

higher survival going forward. This may also explain why we did not see the effect of birth type in the survival analyses, which take into account which portions of the lifespan are observed and therefore provide more robust results. As such, we urge caution against over-interpretation of the results that may suggest that wild-born chimpanzees have some form of extra resilience that boosts their longevity.

We also examined how life history characteristics may have changed over time by comparing data from an early period (1975/1980-2000) to a later period (2001-2020). In both regions, age at death has increased in the most recent 20-year period compared to the two decades prior. However, it is important to note that this only represents deaths that had occurred in these periods and because the population was younger overall in the early period, the average age at death was also younger. For example, it does not mean that a captive-born AZA male living in the early time period would only live to 10; rather that captive-born AZA males that died in the early time period were on average aged 10. The median age of both populations is increasing over time (Fig. 3.3) and will likely continue to increase as more animals have the chance to live out their lifespan. These results demonstrate that focusing only on ages at death can be misleading for determining animal life expectancy, similar to an earlier study on captive elephants (Wiese & Willis, 2004). This artefact also makes it difficult to test whether there are differences in survival over time due to advancements in care and management protocols as well as veterinary capabilities over the past forty years. In the AZA population for instance, there have been significant improvements in a number of aspects of behavioral management including the promotion of larger and more natural (e.g. multimale) groups and the integration of fission-fusion management systems that may promote a more natural social setting for zoo-housed chimpanzees. Likewise, veterinary expertise surrounding sedation protocols (Naples, Langan &

Kearns, 2010), diet (Struck et al., 2007) and wound management (Baker et al., 2000) may contribute to improving health, welfare and potentially longevity in recent years. Similar activities are being done in Japan as well to promote environmental enrichment (Morimura & Ueno, 1999; Morimura, 2003), stress monitoring (Yamanashi et al., 2013), method of sedation (Miyabe-Nishiwaki et al., 2021), and detection of zoonotic pathogens (Kooriyama et al., 2013).

Finally, we validated the findings of Havercamp et al. (2019) showing that chimpanzees in the Japan population were more likely to die in winter months. For the AZA population, our data suggest that deaths may peak in both the winter and summer periods (compared to spring and autumn; Fig. 3.4) but this seasonal pattern was not statistically significant. Although Japan is geographically much smaller than America, both countries are characterized by a broad degree of climatic variation. We are unable to specify if such impacts are particularly prevalent in regions which experience particularly cold winters, though further detailed study of these climate-related effects would be welcome. Nonetheless, these findings provide further support that husbandry efforts should be intensified during the winter season (e.g. continuous availability of temperature controlled rooms, special diet, warming enrichment, additional health monitoring), especially towards infants, as chimpanzees are likely not well adapted to cold weather and its effects on health. The challenges of managing chimpanzees, who have evolved in equatorial climates, in winter times remains an important consideration.

3.5 Conclusions

We compiled the largest dataset on chimpanzee life history, consisting of nearly 1400 individuals and spanning four decades, and compared life history patterns in captive chimpanzee populations from two different regions. Despite some differences in management practices, the overall life expectancy and survival patterns were similar between the two regions. However,

survivorship was lower for males than for females in the AZA population but similar among sexes in the Japan population. The Kaplan-Meier median life expectancy from birth was 35.7 (32.4-40.0) years for females and 30.1 (27.3-34.3) years for males across both populations, which is higher than most longevity estimates reported for wild chimpanzees. Birth type (wild-born or captive-born) did not influence survival patterns in either population, and the seasonal death pattern previously shown in the Japan population was not found in the AZA population. We were unable to fully assess changes in survival over time due to the long lifespan of the species and many individuals having yet to live out their full lives. Moreover, our current estimates of median life expectancy will likely increase in future investigations as animals continue to age in both populations. The opportunity to quantitatively compare life history patterns between large populations of managed species is relatively rare, especially with large and long-lived animals such as chimpanzees. Further investigation will increase the potential of these data to inform important population management strategies.

3.6 Figures

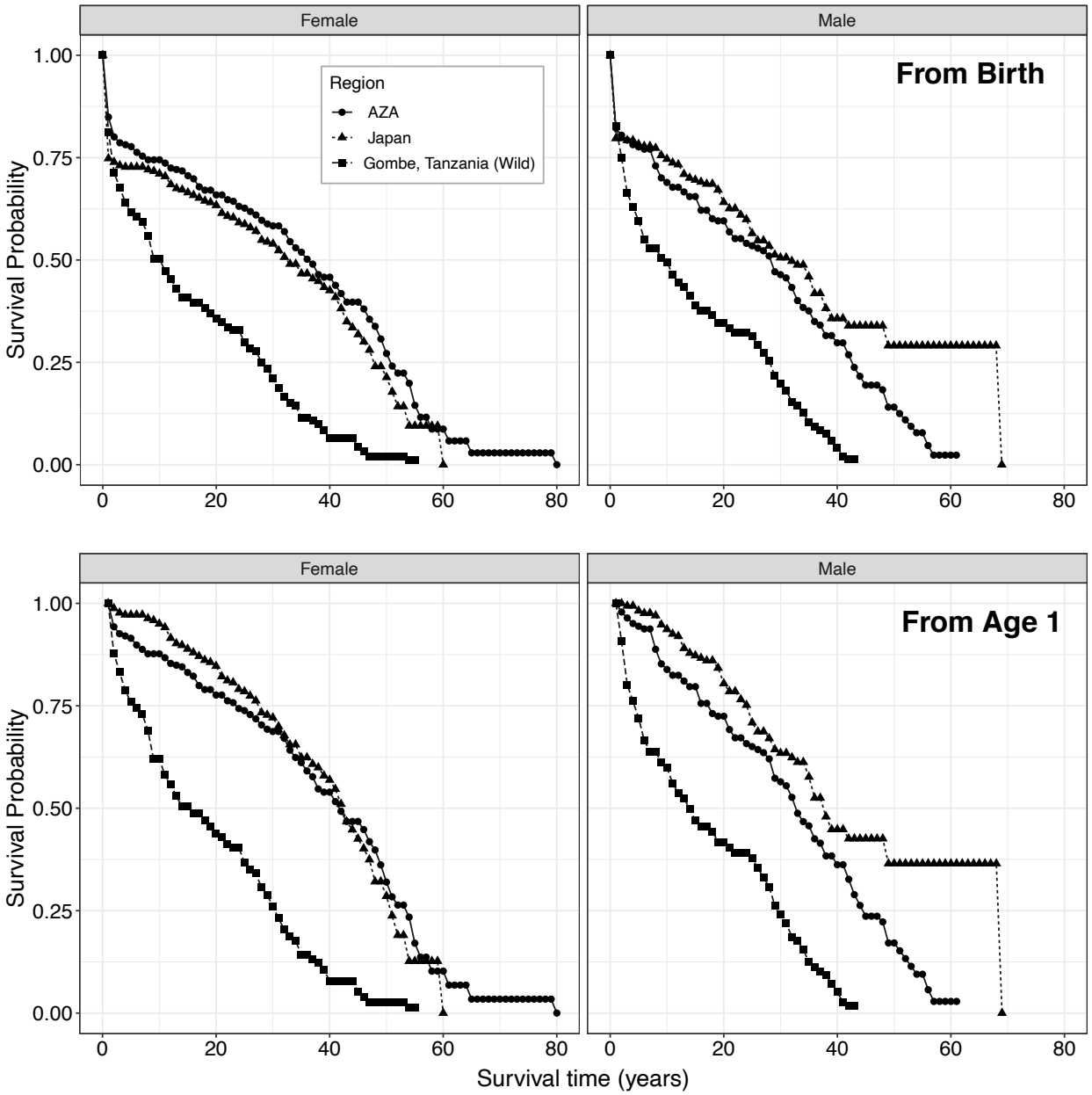

Fig. 3.1 Age-specific survival rates for females (left panels) and males (right panels), from life tables for a wild population and the AZA and Japan captive populations of chimpanzees from birth (top) and from age 1 (bottom). Wild population data is from Gombe, Tanzania (Bronikowski et al. 2016).

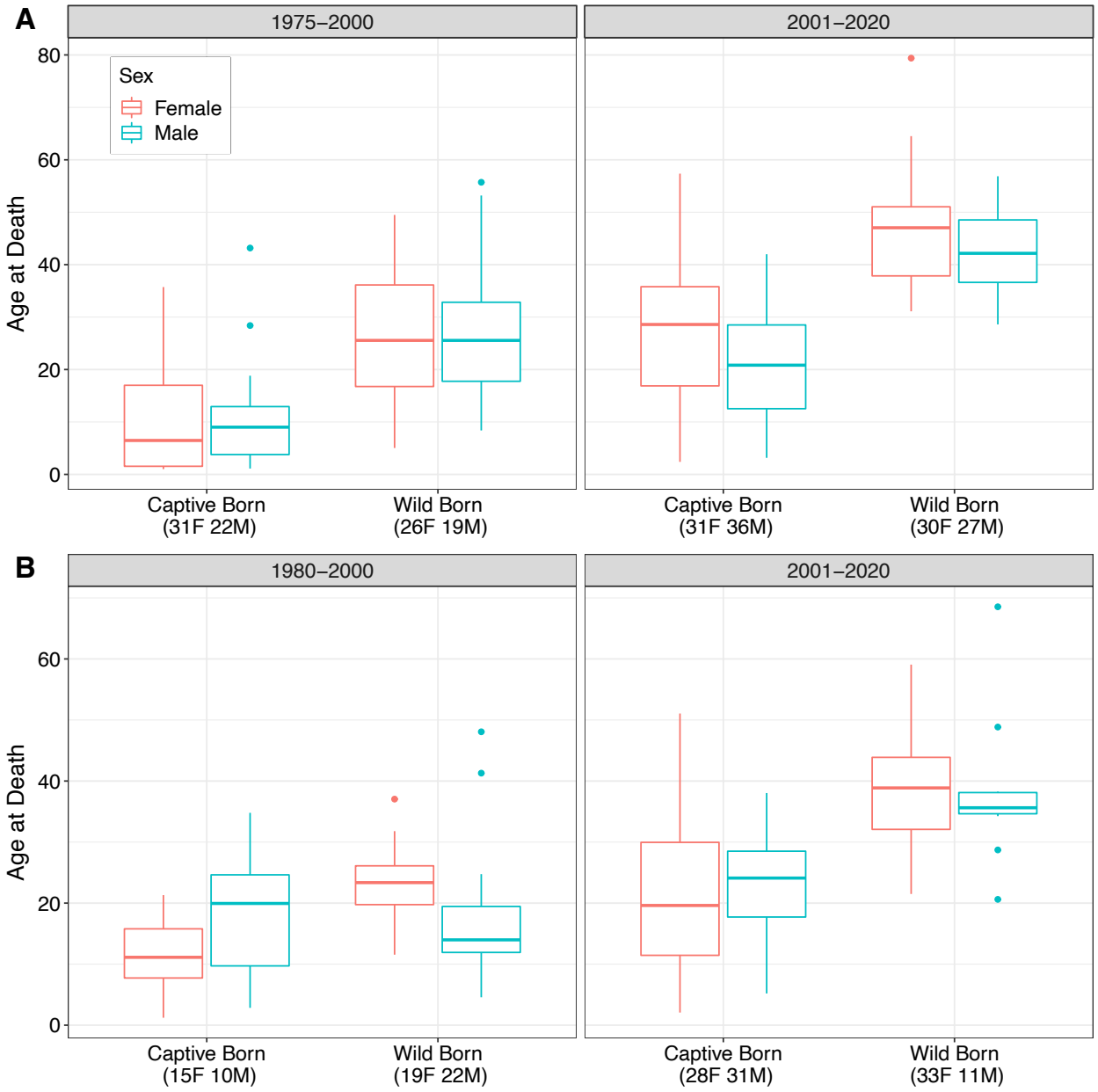

Fig. 3.2 Observed distribution of ages at death by sex, time period, and birth type in (A) the AZA and (B) the Japan captive chimpanzee populations. Only deaths occurring on or after age one are included. The "early" time period is 1975-2000 for AZA and 1980-2000 for Japan, and the "recent" period is 2001-2020 for both. Sample sizes for the number of observed deaths for

females and males are included in parentheses for each group. Note that the y-axis range differs between panels.

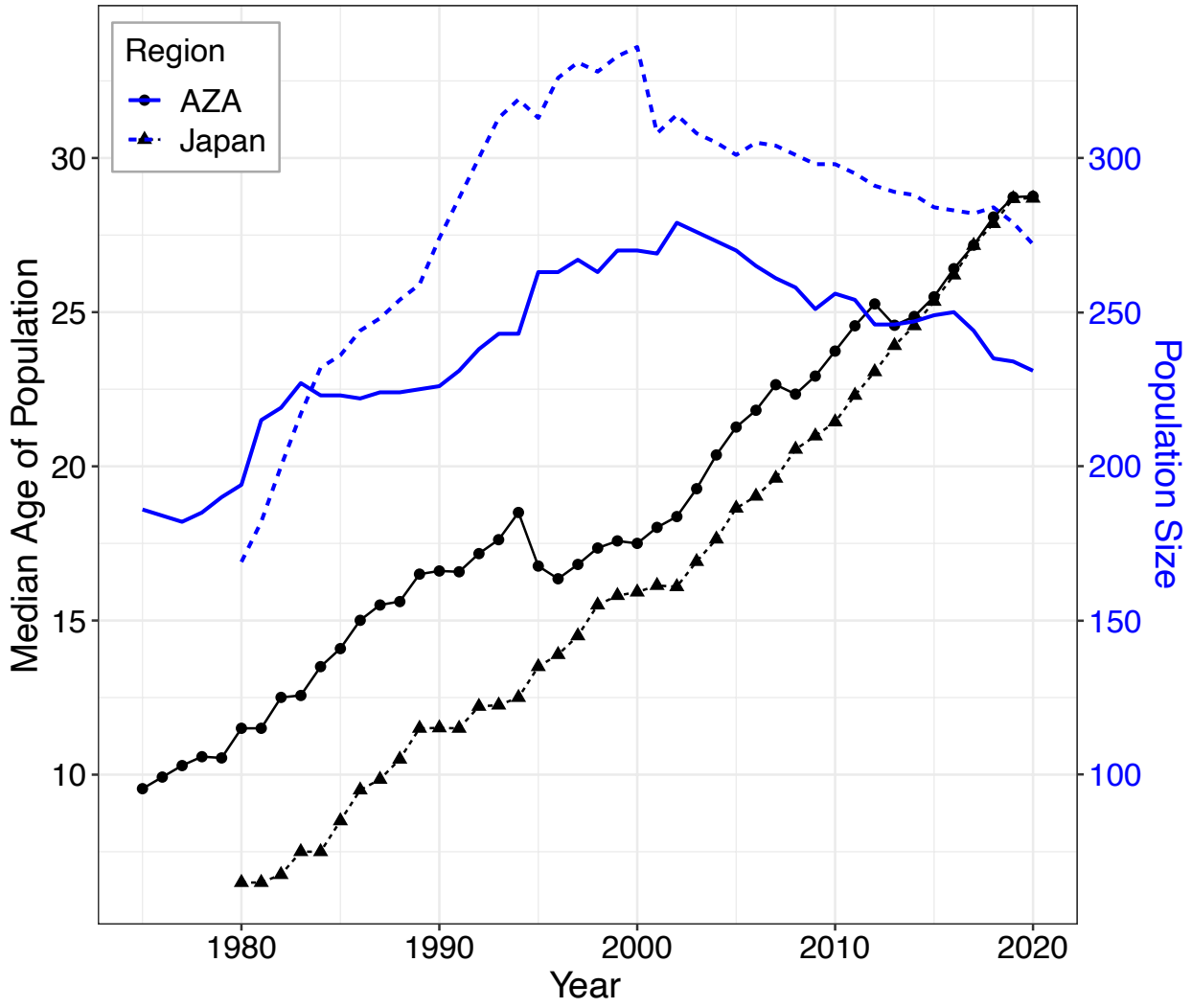

Fig. 3.3 Median age and total population size of the AZA and Japan captive chimpanzee populations over time. Ages were tabulated starting at age one and censused at Dec. 31 of each year (except for the last year, which was censused on the last data compilation date of 2/1/2020).

Individuals who had not yet reached age one or had an unknown birth location (30 individuals in the Japan population and 6 in the AZA population as of Feb. 2020) were not included in this figure.

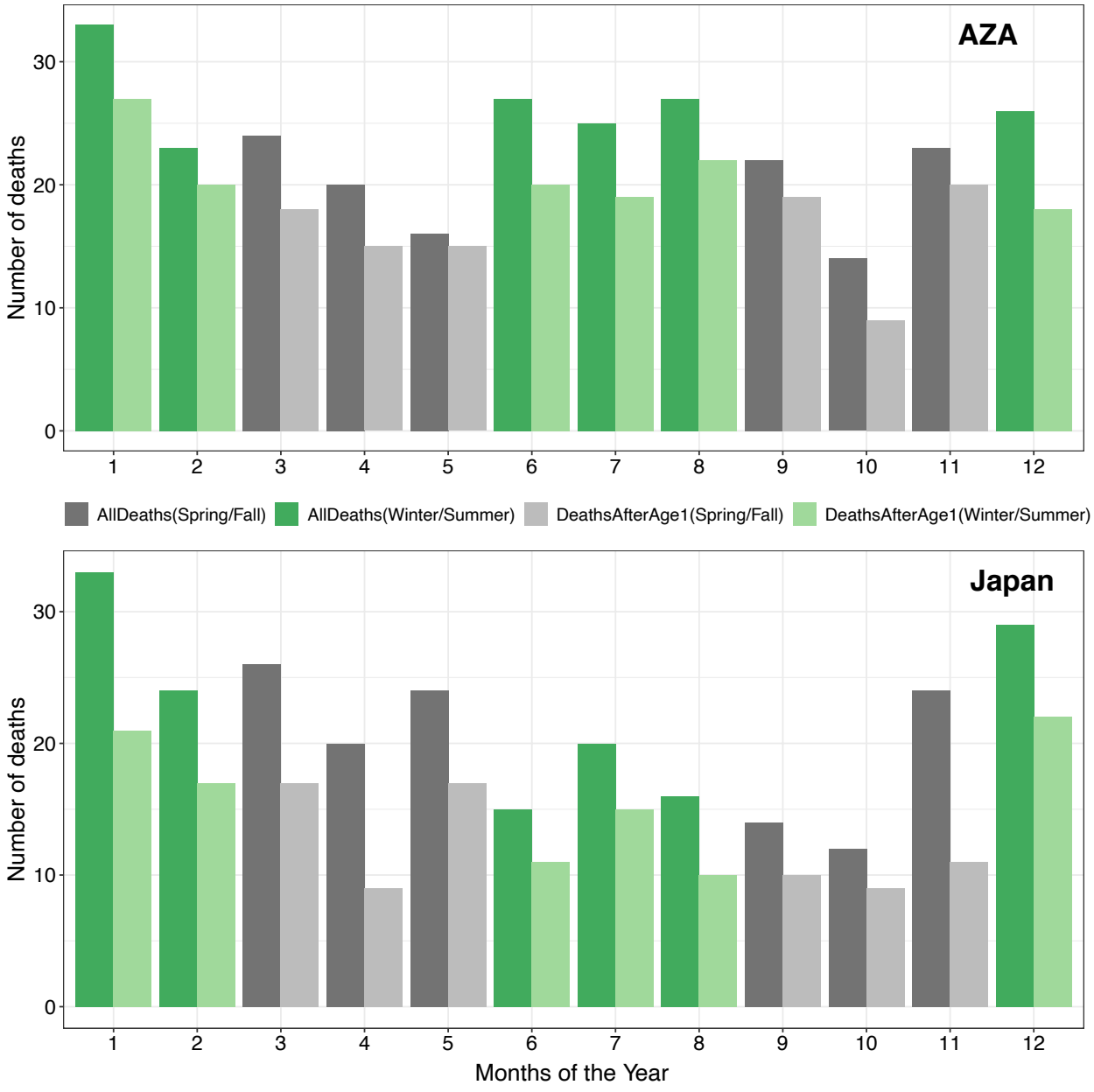

Fig. 3.4 Numbers of deaths in the AZA (top panel) and the Japan (bottom panel) captive chimpanzee populations by month (AZA: 1975–2020, Japan: 1980-2020). Seasons are grouped

in alternating colors: winter = Dec–Feb (green); spring = Mar–May (gray); summer = Jun–Aug (green); Fall = Sep–Nov (gray). Darker bars include all observed deaths, and lighter bars include only deaths on or after age one.

3.7 Tables

Table 3.1 Summary of existing studies describing wild or captive chimpanzee life history patterns. When full life tables are presented for both females and males, life expectancy estimates are combined.

Source	**Population (captive or wild)**	**Location**	**Sample size**	**Life expectancy of live born individuals**	**Life expectancy of individuals who survived beyond 1 year (calculated from life table)**
Havercamp et al. 2019	Captive	Japan 1921-2018	821	Both (sexes) = 28.3y	From 1y = 34.6y From 12y = 40.4y From 15y = 42.4y
Littleton 2005	Captive	Australia 1941-2000	113	Not presented, no life table	Not presented
Dyke et al. 1995	Captive	3 breeding colonies in the United States (years unknown)	F = 650 (Total N = 1,346, but e_x not provided for males)	Females only (observed data) = 23.1y, not reliable due to young population at the time	Not presented – Only model life tables presented
Courtney & Santow 1989	Captive	Australia & New Zealand 1935-1983	87	Not possible to calculate late life expectancy due to small, young	Not presented

				population (mortality probabilities up to 30y presented)	
Wood et al. 2017	Wild	Ngogo, Uganda 1995-2016	306	Both = 32.8y	From 1y = 38.6y From 12y = 43.1y From 15y = 43.1y
Bronikowski et al. 2016	Wild	Gombe, Tanzania 1963-2013	F = 155 (Total N = 288, but e_x not provided for males)	Females only = 15.9y	Females only = From 1y = 19.4y From 12y = 30.2y From 15y = 32.0y
Bronikowski et al. 2011	Wild	Gombe, Tanzania 1963-2008	F = 144 M = 122	Females = 16y (range: 10-25y) Males = 11y (range: 9-14y)	Not presented
Muller & Wrangham 2014	Wild	Kanyawara, Uganda 1989-2013	123	Both = 19.4y	From 1y = 22y From 12y = 34.5y From 15y = 39.2y
Hill et al. 2001	Wild	5 study populations Gombe, Tanzania: 1963-1998; Taï, Ivory Coast: 1982-1994; Kanyawara, Uganda: 1989-1998; Mahale, Tanzania: K group 1966-1988, M group 1979-1988;	179 + 123 + 74 + 92 + 22 = 490	Both = 12.9y	From 1y = 15.6y From 12y = 27.4y From 15y = 29.8y

		Bossou, Guinea: 1976-1993			

Table 3.2 Kaplan-Meier median life expectancy (MLE) estimates for the AZA population (1975–2020), the Japan population (1980–2020), and both populations of captive chimpanzees combined. Separate estimates are presented for females and males and starting from birth or from age one (i.e., assuming survival to first birthday), with their 95% confidence intervals in parentheses. For the Japan population male estimate, the upper limit was undefined because many older males are still living.

	Female MLE	Male MLE
From birth		
AZA	36.7 (32.7-42.1)	28.4 (21.7-32.5)
Japan	34.1 (30.2-41.2)	34.0 (27.1-38.0)
AZA + Japan	35.7 (32.4-40.0)	30.1 (27.3-34.3)
From age one		
AZA	41.9 (37.4-47.5)	32.5 (29.4-37.5)
Japan	42.4 (39.9-47.2)	37.7 (34.8-NA)
AZA + Japan	42.4 (40.0-46.3)	35.5 (32.6-38.0)

Table 3.3 Results from Poisson regressions comparing whether the median age at mortality in the AZA and Japan populations differed based on sex, birth type, and between two time periods in captive chimpanzees. The "early" time period is 1975-2000 for AZA and 1980-2000 for Japan, the "recent" period is 2001-2020 for both. Analyses were performed using only mortalities that occurred on or after the first birthdate. Bolded coefficient estimates highlight the effects that were significant at $p<0.05$.

AZA

	Estimate	Std. Error	z value	p value
(Intercept)	**2.41**	0.12	20.75	< 2E-16
Sex (Male)	-0.08	0.15	-0.53	0.5951
Period (Late)	**0.89**	0.13	6.82	9.33E-11
Birth type (Wild)	**0.87**	0.13	6.5	5.52E-10
Sex (Male) * Period (Late)	-0.16	0.14	-1.18	0.2407
Period (Late) * Birth type (Wild)	**-0.32**	0.14	-2.19	0.0297
Sex (Male) * Birth type (Wild)	0.13	0.13	0.97	0.3319
Null deviance: 2528.3 on 221 degrees of freedom				
Residual deviance: 1255.8 on 215 degrees of freedom				
Dispersion parameter for quasipoisson family taken to be 5.782681				

Japan

	Estimate	Std. Error	z value	p value
(Intercept)	**2.42**	0.16	15.41	< 2E-16
Sex (Male)	**0.46**	0.22	2.08	0.0388
Period (Late)	**0.68**	0.18	3.83	0.0002
Birth type (Wild)	**0.71**	0.19	3.83	0.0002
Sex (Male) * Period (Late)	-0.43	0.25	-1.73	0.0863
Sex (Male) * Birth type (Wild)	**-0.73**	0.26	-2.78	0.0061
Period (Late) * Birth type (Wild)	-0.15	0.21	-0.74	0.4631
Sex * Birth type * Period	**0.69**	0.31	2.24	0.0263
Null deviance: 1203.96 on 168 degrees of freedom				
Residual deviance: 686.09 on 161 degrees of freedom				
Dispersion parameter for quasipoisson family taken to be 4.176631				

3.8 Supplementary Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.11913#supplemental-information.

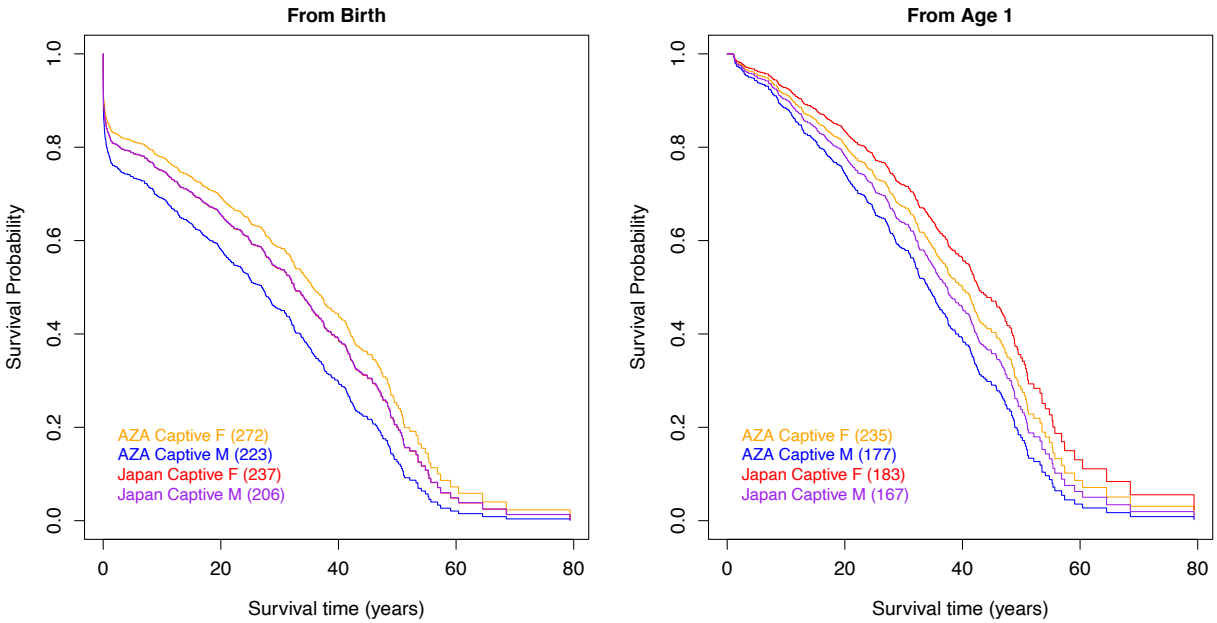

Figure 3.S1 Modeled survival curves based on Cox proportional hazards model for females and males in AZA (1975–2020) and Japan (1980–2020) captive chimpanzee populations, starting from birth (left) or from age one (right). Confidence intervals not shown as they overlap and obscure patterns. Note that the model for survival curves from birth (left) included the interaction between region and sex, whereas the model from age one (right) included no interaction effects. Because there was no significant difference between the sexes in survival from birth for the Japan population, the Japan male and female (red and purple) lines are overlapping in the left panel.

Table 3.S1 AZA captive chimpanzee life table (1975–2020).

In these life tables (Table 3.S1 and Table 3.S2), nx (qx) = number of individuals at risk for mortality calculations, dx = probability of death between age x and x + 1 calculated as l(x+1)-l(x), qx = probability of death between age x and x + 1 calculated as the number of animals that die during an age class divided by the number of animals at risk, lx (0y) = probability of survival from birth to age x, lx (1y) = probability of survival from 1 year to age x, ex = remaining life expectancy (in years) at age x, nx (mx) = number of individuals at risk for fecundity calculations, mx = fecundity or the average number of same-sex young born to individuals in that age class.

	Females								**Males**							
Age (years)	nx (qx)	dx	qx	lx (0yr)	lx (1yr)	ex	nx (mx)	mx	nx (qx)	dx	qx	lx (0yr)	lx (1yr)	ex	nx (mx)	mx
0	179.4	0.15	0.15	1.00		32.9	179.4	0.00	151	0.18	0.18	1.00		27.1	151	0.00
1	169.9	0.05	0.06	0.85	1.00	37.6	169.9	0.00	137.6	0.02	0.02	0.82	1.00	31.7	137.6	0.00
2	167.2	0.01	0.02	0.80	0.94	38.8	167.2	0.00	134.6	0.01	0.02	0.80	0.98	31.4	134.6	0.00
3	168.6	0.00	0.01	0.79	0.93	38.5	168.6	0.00	138	0.01	0.01	0.79	0.96	30.8	138	0.00
4	166	0.00	0.01	0.78	0.92	37.8	166	0.00	135	0.01	0.01	0.78	0.95	30.3	135	0.00
5	170.8	0.01	0.02	0.78	0.91	37.0	170.8	0.00	134.3	0.01	0.01	0.78	0.94	29.5	134.3	0.00
6	170.8	0.01	0.01	0.76	0.90	36.6	170.8	0.00	131	0.00	0.00	0.77	0.94	28.7	131	0.01
7	169	0.01	0.01	0.75	0.89	36.1	169	0.02	127.2	0.04	0.05	0.77	0.94	27.7	127.2	0.06
8	170	0.00	0.00	0.74	0.88	35.5	170	0.04	122.9	0.03	0.04	0.73	0.89	28.2	122.9	0.06
9	168.4	0.00	0.00	0.74	0.88	34.5	168.4	0.04	120.6	0.01	0.02	0.70	0.85	28.3	120.6	0.10
10	175.1	0.01	0.01	0.74	0.88	33.5	175.1	0.07	117.8	0.01	0.02	0.69	0.84	27.8	117.8	0.12
11	179.2	0.01	0.02	0.74	0.87	32.9	179.2	0.05	113.5	0.00	0.00	0.68	0.82	27.2	113.5	0.08
12	184.9	0.00	0.01	0.72	0.85	32.4	184.9	0.07	115.9	0.01	0.02	0.68	0.82	26.2	115.9	0.11
13	184.5	0.00	0.01	0.72	0.85	31.5	184.5	0.06	116.4	0.01	0.02	0.67	0.81	25.6	116.4	0.08
14	180.9	0.01	0.02	0.72	0.85	30.7	180.9	0.04	116.5	0.00	0.00	0.65	0.80	25.1	116.5	0.07
15	178.4	0.01	0.01	0.71	0.83	30.2	178.4	0.05	114	0.03	0.05	0.65	0.80	24.1	114	0.08

16	177	0.02	0.03	0.70	0.82	29.5	177	0.05	116.3	0.00	0.00	0.62	0.76	24.3	116.3	0.05
17	173.2	0.01	0.01	0.68	0.80	29.3	173.2	0.04	117.9	0.02	0.03	0.62	0.76	23.3	117.9	0.11
18	173.5	0.00	0.00	0.67	0.79	28.7	173.5	0.03	111.9	0.01	0.01	0.60	0.73	23.1	111.9	0.08
19	172.6	0.01	0.02	0.67	0.79	27.7	172.6	0.05	110.3	0.00	0.00	0.60	0.72	22.3	110.3	0.08
20	164.9	0.00	0.00	0.66	0.78	27.1	164.9	0.03	108.7	0.03	0.05	0.60	0.72	21.3	108.7	0.09
21	160.8	0.01	0.02	0.66	0.78	26.1	160.8	0.03	100.8	0.02	0.03	0.57	0.69	21.2	100.8	0.08
22	156.9	0.00	0.01	0.65	0.76	25.6	156.9	0.06	97.2	0.00	0.00	0.55	0.67	20.8	97.2	0.04
23	152.6	0.01	0.02	0.64	0.76	24.7	152.6	0.05	95.4	0.01	0.02	0.55	0.67	19.8	95.4	0.11
24	151.3	0.00	0.01	0.63	0.74	24.2	151.3	0.03	89.8	0.01	0.01	0.54	0.66	19.2	89.8	0.05
25	148.5	0.01	0.01	0.63	0.74	23.4	148.5	0.05	86.7	0.01	0.01	0.53	0.65	18.4	86.7	0.05
26	145	0.01	0.01	0.62	0.73	22.6	145	0.05	84.3	0.01	0.01	0.53	0.64	17.6	84.3	0.08
27	140.8	0.01	0.02	0.61	0.72	22.0	140.8	0.02	81.2	0.01	0.02	0.52	0.64	16.8	81.2	0.03
28	135.4	0.01	0.02	0.60	0.70	21.4	135.4	0.03	75.5	0.04	0.08	0.51	0.62	16.2	75.5	0.02
29	127.8	0.00	0.01	0.59	0.69	20.7	127.8	0.02	67.4	0.01	0.02	0.47	0.57	16.5	67.4	0.04
30	124.1	0.00	0.00	0.58	0.69	19.9	124.1	0.02	60.9	0.01	0.02	0.46	0.56	15.7	60.9	0.02
31	120.1	0.01	0.02	0.58	0.69	18.9	120.1	0.03	57.1	0.02	0.05	0.46	0.56	15.0	57.1	0.03
32	113.6	0.02	0.04	0.57	0.67	18.3	113.6	0.02	51.8	0.03	0.07	0.43	0.53	14.7	51.8	0.06
33	104	0.02	0.03	0.54	0.64	18.1	104	0.01	47.9	0.02	0.04	0.40	0.49	14.8	47.9	0.02
34	97.5	0.01	0.02	0.53	0.62	17.6	97.5	0.03	45.8	0.01	0.02	0.38	0.47	14.4	45.8	0.03
35	89	0.02	0.03	0.52	0.61	16.9	89	0.02	42	0.03	0.07	0.38	0.46	13.7	42	0.00
36	82	0.01	0.02	0.50	0.59	16.5	82	0.01	39.2	0.01	0.03	0.35	0.43	13.7	39.2	0.03
37	75.2	0.03	0.05	0.49	0.58	15.8	75.2	0.01	38.2	0.03	0.08	0.34	0.41	13.0	38.2	0.00
38	72.8	0.01	0.01	0.46	0.55	15.7	72.8	0.03	37.3	0.00	0.00	0.32	0.38	13.0	37.3	0.01
39	71.5	0.00	0.00	0.46	0.54	14.9	71.5	0.01	34.8	0.02	0.06	0.32	0.38	12.0	34.8	0.02
40	67.2	0.02	0.04	0.46	0.54	13.9	67.2	0.05	34	0.00	0.00	0.30	0.36	11.6	34	0.02
41	63.6	0.02	0.05	0.44	0.52	13.4	63.6	0.02	29.7	0.03	0.10	0.30	0.36	10.6	29.7	0.02
42	58.1	0.02	0.05	0.42	0.49	13.0	58.1	0.00	23.5	0.03	0.12	0.27	0.33	10.7	23.5	0.00
43	55.7	0.00	0.00	0.40	0.47	12.7	55.7	0.01	20.8	0.02	0.09	0.24	0.29	10.9	20.8	0.03
44	52.4	0.00	0.00	0.40	0.47	11.7	52.4	0.00	19.2	0.02	0.10	0.22	0.26	10.9	19.2	0.00

45	49.8	0.02	0.04	0.40	0.47	10.7	49.8	0.00	19	0.00	0.00	0.19	0.24	11.0	19	0.03
46	44.2	0.03	0.07	0.38	0.45	10.1	44.2	0.00	18.4	0.00	0.00	0.19	0.24	10.0	18.4	0.00
47	38.8	0.02	0.05	0.36	0.42	9.8	38.8	0.01	15	0.01	0.06	0.19	0.24	9.0	15	0.03
48	31.9	0.03	0.09	0.34	0.40	9.2	31.9	0.00	12.4	0.04	0.23	0.18	0.22	8.5	12.4	0.00
49	25	0.04	0.12	0.31	0.36	9.0	25	0.00	9.6	0.00	0.00	0.14	0.17	9.8	9.6	0.00
50	17.8	0.03	0.11	0.27	0.32	9.1	17.8	0.04	8.2	0.02	0.11	0.14	0.17	8.8	8.2	0.07
51	12.4	0.02	0.07	0.24	0.28	9.1	12.4	0.00	7.1	0.02	0.13	0.13	0.15	8.7	7.1	0.00
52	9.6	0.00	0.00	0.22	0.26	8.7	9.6	0.00	6.2	0.02	0.14	0.11	0.13	8.9	6.2	0.00
53	8.6	0.02	0.11	0.22	0.26	7.7	8.6	0.00	5.2	0.02	0.17	0.09	0.11	9.2	5.2	0.00
54	6.6	0.05	0.27	0.20	0.23	7.6	6.6	0.00	5	0.00	0.00	0.08	0.10	9.8	5	0.00
55	4.4	0.03	0.20	0.15	0.17	9.0	4.4	0.00	4	0.03	0.40	0.08	0.10	8.8	4	0.00
56	4	0.00	0.00	0.12	0.14	10.0	4	0.13	2.5	0.02	0.50	0.05	0.06	13.0	2.5	0.00
57	3.4	0.03	0.25	0.12	0.14	9.0	3.4	0.00	1	0.00	0.00	0.02	0.03	24.0	1	0.00
58	3	0.00	0.00	0.09	0.10	10.7	3	0.00	1	0.00	0.00	0.02	0.03	23.0	1	0.00
59	3	0.00	0.00	0.09	0.10	9.7	3	0.17	1	0.00	0.00	0.02	0.03	22.0	1	0.00
60	2.5	0.03	0.33	0.09	0.10	8.7	2.5	0.00	1	0.00	0.00	0.02	0.03	21.0	1	0.00
61	2	0.00	0.00	0.06	0.07	11.5	2	0.25	0.6	0.00	0.00	0.02	0.03	20.0	0.6	0.00
62	2	0.00	0.00	0.06	0.07	10.5	2	0.25	0	0.00	0.00	0.02	0.03	19.0	0	0.00
63	2	0.00	0.00	0.06	0.07	9.5	2	0.00	0	0.00	0.00	0.02	0.03	18.0	0	0.00
64	1.6	0.03	0.50	0.06	0.07	8.5	1.6	0.00	0	0.00	0.00	0.02	0.03	17.0	0	0.00
65	1	0.00	0.00	0.03	0.03	15.0	1	0.00	0	0.00	0.00	0.02	0.03	16.0	0	0.00
66	1	0.00	0.00	0.03	0.03	14.0	1	0.00	0	0.00	0.00	0.02	0.03	15.0	0	0.00
67	1	0.00	0.00	0.03	0.03	13.0	1	0.00	0	0.00	0.00	0.02	0.03	14.0	0	0.00
68	1	0.00	0.00	0.03	0.03	12.0	1	0.00	0	0.00	0.00	0.02	0.03	13.0	0	0.00
69	1	0.00	0.00	0.03	0.03	11.0	1	0.00	0	0.00	0.00	0.02	0.03	12.0	0	0.00
70	1	0.00	0.00	0.03	0.03	10.0	1	0.00	0	0.00	0.00	0.02	0.03	11.0	0	0.00
71	1	0.00	0.00	0.03	0.03	9.0	1	0.00	0	0.00	0.00	0.02	0.03	10.0	0	0.00
72	1	0.00	0.00	0.03	0.03	8.0	1	0.00	0	0.00	0.00	0.02	0.03	9.0	0	0.00
73	1	0.00	0.00	0.03	0.03	7.0	1	0.00	0	0.00	0.00	0.02	0.03	8.0	0	0.00

74	1	0.00	0.00	0.03	0.03	6.0	1	0.00	0	0.00	0.00	0.02	0.03	7.0	0	0.00
75	1	0.00	0.00	0.03	0.03	5.0	1	0.00	0	0.00	0.00	0.02	0.03	6.0	0	0.00
76	1	0.00	0.00	0.03	0.03	4.0	1	0.00	0	0.00	0.00	0.02	0.03	5.0	0	0.00
77	1	0.00	0.00	0.03	0.03	3.0	1	0.00	0	0.00	0.00	0.02	0.03	4.0	0	0.00
78	1	0.00	0.00	0.03	0.03	2.0	1	0.00	0	0.00	0.00	0.02	0.03	3.0	0	0.00
79	0	0.03	1.00	0.03	0.03	1.0	0	0.00	0	0.00	0.00	0.02	0.03	2.0	0	0.00
80	0	0.00	1.00	0.00	0.00		0	0.00	0	0.00	0.00	0.02	0.03	1.0	0	0.00

Table 3.S2 Japan captive chimpanzee life table (1980–2020). Please see Table 3.S1 legend for definitions of abbreviated terms.

	Females						Males								
Age (years)	nx (qx)	dx	qx	lx (0yr)	lx (1yr)	ex	nx (mx)	mx	nx (qx)	dx	qx	lx (0yr)	lx (1yr)	ex	nx (mx)	mx
0	163.3	0.25	0.25	1.00		29.5	163.3	0.00	147.6	0.20	0.20	1.00		34.3	147.6	0.00
1	171.7	0.01	0.01	0.75	1.00	38.1	171.7	0.00	152	0.00	0.00	0.80	1.00	41.8	152	0.00
2	186.4	0.01	0.01	0.74	0.99	37.5	186.4	0.00	165.5	0.00	0.01	0.80	1.00	40.8	165.5	0.00
3	193.4	0.00	0.01	0.73	0.98	37.0	193.4	0.00	170.6	0.00	0.00	0.79	0.99	40.1	170.6	0.00
4	202.9	0.00	0.00	0.73	0.97	36.1	202.9	0.00	171.2	0.01	0.01	0.79	0.99	39.1	171.2	0.00
5	211.6	0.00	0.00	0.73	0.97	35.1	211.6	0.00	172.4	0.00	0.01	0.78	0.98	38.5	172.4	0.00
6	215.5	0.00	0.00	0.73	0.97	34.1	215.5	0.01	175	0.00	0.00	0.78	0.98	37.8	175	0.00
7	217.7	0.01	0.01	0.73	0.97	33.1	217.7	0.00	174	0.00	0.01	0.78	0.98	36.8	174	0.01
8	217.9	0.00	0.01	0.72	0.96	32.4	217.9	0.02	173.9	0.02	0.02	0.77	0.97	36.0	173.9	0.04
9	218.8	0.01	0.01	0.72	0.96	31.6	218.8	0.03	171.6	0.01	0.01	0.76	0.95	35.8	171.6	0.06
10	217.2	0.01	0.01	0.71	0.95	30.9	217.2	0.06	169.3	0.01	0.01	0.75	0.94	35.2	169.3	0.07
11	212.4	0.02	0.03	0.70	0.94	30.1	212.4	0.06	162.9	0.00	0.01	0.74	0.93	34.6	162.9	0.09
12	209.3	0.01	0.01	0.68	0.92	30.0	209.3	0.05	154.9	0.02	0.03	0.73	0.92	33.8	154.9	0.09
13	205	0.00	0.01	0.67	0.90	29.4	205	0.06	149.3	0.01	0.01	0.71	0.89	33.9	149.3	0.08
14	200.7	0.01	0.01	0.67	0.90	28.5	200.7	0.06	145.1	0.00	0.01	0.70	0.88	33.4	145.1	0.08
15	196.8	0.01	0.01	0.66	0.89	27.8	196.8	0.05	142.8	0.00	0.01	0.70	0.87	32.6	142.8	0.05
16	194.6	0.01	0.01	0.66	0.88	27.1	194.6	0.05	141.8	0.00	0.01	0.69	0.87	31.8	141.8	0.07
17	188.4	0.01	0.01	0.65	0.87	26.3	188.4	0.08	141.4	0.00	0.00	0.69	0.86	31.0	141.4	0.05
18	180.8	0.00	0.01	0.64	0.86	25.6	180.8	0.03	138	0.01	0.02	0.69	0.86	30.0	138	0.06
19	175.4	0.01	0.01	0.64	0.86	24.8	175.4	0.05	130.7	0.03	0.05	0.67	0.84	29.7	130.7	0.08
20	168.1	0.02	0.03	0.63	0.85	24.0	168.1	0.04	123	0.02	0.02	0.64	0.80	30.0	123	0.09
21	158.9	0.01	0.01	0.61	0.82	23.7	158.9	0.04	120	0.00	0.00	0.63	0.79	29.7	120	0.04

22	154.2	0.00	0.01	0.61	0.81	23.0	154.2	0.04	117.8	0.02	0.03	0.63	0.79	28.7	117.8	0.04
23	151.8	0.01	0.02	0.60	0.81	22.2	151.8	0.04	113	0.01	0.02	0.61	0.77	28.4	113	0.03
24	147.2	0.00	0.01	0.59	0.79	21.6	147.2	0.03	104	0.03	0.06	0.60	0.75	27.9	104	0.03
25	140.4	0.01	0.01	0.59	0.79	20.7	140.4	0.03	93.5	0.02	0.03	0.57	0.71	28.6	93.5	0.04
26	137.8	0.01	0.02	0.58	0.77	20.0	137.8	0.03	90.5	0.00	0.00	0.55	0.69	28.4	90.5	0.02
27	128.1	0.02	0.04	0.57	0.76	19.3	128.1	0.01	82.2	0.01	0.02	0.55	0.69	27.4	82.2	0.04
28	119.8	0.00	0.01	0.55	0.73	19.0	119.8	0.03	73.4	0.02	0.04	0.53	0.67	27.1	73.4	0.07
29	109.2	0.00	0.01	0.54	0.73	18.2	109.2	0.02	66.8	0.01	0.01	0.51	0.64	27.2	66.8	0.05
30	101.6	0.02	0.03	0.54	0.72	17.3	101.6	0.03	61.5	0.00	0.00	0.51	0.63	26.6	61.5	0.03
31	95.4	0.02	0.03	0.52	0.70	16.8	95.4	0.01	59.4	0.01	0.02	0.51	0.63	25.6	59.4	0.03
32	87.5	0.02	0.03	0.51	0.68	16.3	87.5	0.06	55.7	0.01	0.02	0.50	0.62	25.0	55.7	0.08
33	85	0.00	0.00	0.49	0.66	15.9	85	0.04	51	0.00	0.00	0.49	0.61	24.4	51	0.04
34	81.5	0.02	0.05	0.49	0.66	14.9	81.5	0.02	48.3	0.03	0.06	0.49	0.61	23.4	48.3	0.03
35	78.5	0.00	0.00	0.47	0.62	14.6	78.5	0.02	43	0.04	0.09	0.46	0.58	23.8	43	0.05
36	75.2	0.01	0.03	0.47	0.62	13.6	75.2	0.03	39.2	0.00	0.00	0.42	0.53	25.1	39.2	0.03
37	66.1	0.01	0.01	0.45	0.61	12.9	66.1	0.04	34.8	0.04	0.09	0.42	0.53	24.1	34.8	0.01
38	61.2	0.01	0.03	0.45	0.60	12.1	61.2	0.03	27.3	0.02	0.07	0.38	0.48	25.2	27.3	0.04
39	56.7	0.01	0.02	0.43	0.58	11.4	56.7	0.04	23.6	0.00	0.00	0.36	0.45	25.9	23.6	0.02
40	50.2	0.02	0.04	0.43	0.57	10.6	50.2	0.01	22.2	0.00	0.00	0.36	0.45	24.9	22.2	0.02
41	43	0.03	0.07	0.41	0.55	10.0	43	0.01	17.9	0.02	0.05	0.36	0.45	23.9	17.9	0.05
42	34.6	0.03	0.08	0.38	0.51	9.7	34.6	0.00	13.6	0.00	0.00	0.34	0.43	24.1	13.6	0.04
43	26.4	0.01	0.04	0.35	0.47	9.5	26.4	0.00	12.6	0.00	0.00	0.34	0.43	23.1	12.6	0.04
44	21.8	0.02	0.05	0.33	0.45	8.8	21.8	0.00	12	0.00	0.00	0.34	0.43	22.1	12	0.04
45	18.3	0.02	0.06	0.32	0.43	8.2	18.3	0.00	10.9	0.00	0.00	0.34	0.43	21.1	10.9	0.00
46	15.9	0.02	0.07	0.30	0.40	7.7	15.9	0.00	8.6	0.00	0.00	0.34	0.43	20.1	8.6	0.06
47	12.5	0.04	0.14	0.28	0.37	7.2	12.5	0.00	8	0.00	0.00	0.34	0.43	19.1	8	0.00
48	10.6	0.00	0.00	0.24	0.32	7.2	10.6	0.00	5.7	0.05	0.14	0.34	0.43	18.1	5.7	0.09
49	7.7	0.03	0.11	0.24	0.32	6.2	7.7	0.00	4.6	0.00	0.00	0.29	0.37	20.0	4.6	0.00
50	5.9	0.04	0.17	0.21	0.29	5.8	5.9	0.00	4	0.00	0.00	0.29	0.37	19.0	4	0.00

51	4.1	0.04	0.20	0.18	0.24	5.8	4.1	0.00	3.5	0.00	0.00	0.29	0.37	18.0	3.5	0.00
52	3.6	0.00	0.00	0.14	0.19	6.0	3.6	0.00	3	0.00	0.00	0.29	0.37	17.0	3	0.00
53	2.6	0.05	0.33	0.14	0.19	5.0	2.6	0.00	2.6	0.00	0.00	0.29	0.37	16.0	2.6	0.00
54	1.6	0.00	0.00	0.09	0.13	6.0	1.6	0.00	2	0.00	0.00	0.29	0.37	15.0	2	0.00
55	1	0.00	0.00	0.09	0.13	5.0	1	0.00	2	0.00	0.00	0.29	0.37	14.0	2	0.00
56	1	0.00	0.00	0.09	0.13	4.0	1	0.00	1.6	0.00	0.00	0.29	0.37	13.0	1.6	0.00
57	1	0.00	0.00	0.09	0.13	3.0	1	0.00	1	0.00	0.00	0.29	0.37	12.0	1	0.00
58	1	0.00	0.00	0.09	0.13	2.0	1	0.00	1	0.00	0.00	0.29	0.37	11.0	1	0.00
59	0.1	0.09	1.00	0.09	0.13	1.0	0.1	0.00	1	0.00	0.00	0.29	0.37	10.0	1	0.00
60	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	9.0	1	0.00
61	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	8.0	1	0.00
62	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	7.0	1	0.00
63	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	6.0	1	0.00
64	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	5.0	1	0.00
65	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	4.0	1	0.00
66	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	3.0	1	0.00
67	0	0.00	1.00	0.00	0.00		0	0.00	1	0.00	0.00	0.29	0.37	2.0	1	0.00
68	0	0.00	1.00	0.00	0.00		0	0.00	0	0.29	1.00	0.29	0.37	1.0	0	0.00
69	0	0.00	1.00	0.00	0.00		0	0.00	0	0.00	1.00	0.00	0.00		0	0.00

3.9 Data Availability

Anonymized, individual-level data and R script for all analyses and figures are available at Figshare: Che–Castaldo, Judy (2021): Comparative survival analyses among captive chimpanzees (*Pan troglodytes*) in America and Japan. DOI 10.6084/m9.figshare.14685429.v1.

Chapter 4

Sleep patterns of aging chimpanzees (*Pan troglodytes*)

4.1 Introduction

Sleep is essential for all primates, and substantial evidence exists linking sleep to the maintenance of the body and the brain including neurogenesis, oxidative stress defense, energy restoration and cognitive processing (e.g. Samson and Nunn 2015; Samson et al. 2019; Siegel 2005; Walker 2008). Primate sleep duration varies greatly across species, from around 7 hours in humans (*Homo sapiens*) to 17 hours in owl monkeys (*Aotus trivirgatus*), with chimpanzees (*Pan troglodytes*) sleeping around 10 hours, just below the average for primates (Nunn and Samson 2018; Nunn et al. 2010). While humans sleep fewer hours than their closest primate relatives, chimpanzees and bonobos (*Pan paniscus*), they obtain overall deeper sleep and a higher proportion of rapid eye movement (REM) sleep, the stage in which dreams typically occur and when animals experience a maximal disconnect from their external environment (Nunn and Samson 2018; Samson and Nunn 2015).

Sleep quality diminishes with healthy aging in humans, with a decrease in total sleep duration, more frequent awakenings, shorter sleep bouts and longer awake bouts (e.g. Floyd et al. 2000; Gulia and Kumar 2018; Li et al. 2018; Mander et al. 2017; Vitiello 1997, 2006). A wide range of species, including geladas (*Theropithecus gelada*; Noser et al. 2003), rhesus macaques (*Macaca mulatta*; Zhdanova et al. 2011), Asian elephants (*Elephas maximus*; Walsh 2017) and even fruit flies (*Drosophila melanogaster*; Koh et al. 2006) also exhibit characteristics of decreasing sleep quality with age such as less or more fragmented sleep. However, we do not know if similar changes occur in our closest evolutionary relatives, with whom we share similar life

history patterns and long periods of sleep. Moreover, because most human sleep studies have focused on individuals from industrialized populations, the sleep behavior of people living in non-industrial or small-scale societies is less well understood. In one study, opposite changes were observed among pastoralists in a small-scale society where labor demands shifted to younger individuals, possibly freeing more time for the elders to sleep (Prall et al. 2018), illustrating that diverse sleep patterns exist across human populations (Rattenborg et al. 2017).

Although sleep is an essential activity which can occupy around half of an individuals' lifetime, the sleep behaviors of chimpanzees and most other primates are not well understood. In the wild, chimpanzees typically select a site suitable for building sleeping platforms in trees usually around 8–20 m high, but up to 48 m high, and sleep in those platforms from dusk to dawn (Goodall 1962; McCarthy et al. 2017). Although chimpanzees are diurnal, various night-time activities have been reported such as vocalizing, urinating, feeding, crop raiding and socializing (Krief et al. 2014; Pruetz 2018; Zamma 2014). Given the sleeping habits of wild chimpanzees, they have never been recorded in detail. Collecting unobstructed night recordings in captive environments can also be challenging, and scoring videos is tedious and time consuming. Recent advances may facilitate captive sleep studies (e.g. Melvin et al. 2019), but describing sleep architecture in the wild will likely remain a challenge for many primate species (but see Reinhardt et al. 2019 for the first detailed sleep study of a primate in the wild using actigraphy). Despite this, the study of sleep in natural environments is encouraged to measure its patterns and functions in the ecological contexts animals evolved in (Rattenborg et al. 2017; Reinhardt 2020).

Although captive chimpanzee sleep patterns have been described non-invasively (Morimura et al. 2012, Videan 2006), little is known about the potential effects of advanced age on their sleep, and no study has followed the same individuals over an extended period of time (i.e.

longitudinal study). In one study, older chimpanzees (33–44 years, N = 10) slept longer and had fewer sleep disruptions than younger, prime adults (14–28 years, N = 10), suggesting that they experienced higher overall sleep quality (Videan 2006). In another report, increasing age resulted in more frequent awakenings, but not a decrease in total sleep time; however, this study did not include individuals old enough (only one, 37 years old) to address potential age effects comprehensively (Morimura et al. 2012).

We studied the sleep of captive chimpanzees living at Kumamoto Sanctuary in Japan and present a cross-sectional and longitudinal investigation of the effects of aging on sleep. Our first aim is to expand the literature on chimpanzee sleep patterns with new data including aged individuals by describing four sleep variables and comparing two age classes (prime and old adults) cross-sectionally. To do this, we video recorded 12 long-term resident male chimpanzees over six, 13-hour nights (resulting in 936 h of data) and analyzed the videos following Morimura et al. (2012), using instantaneous sampling at 1-minute intervals. Our second aim is to examine whether individual sleep quality changes with increasing age, and for this we took a long-term, or follow-up, approach. To do this, we compared our data collected from 2018 to 2019 with data collected from 2007 to 2008 on the same 12 individuals living under the same conditions (Morimura et al. 2012). Thus, we compared repeated measures on the same individuals at two points in time separated by approximately 11 years.

We hypothesize that as chimpanzees age, their sleep quality decreases. Specifically, we predict the following differences in older individuals (cross-sectional comparisons) and changes within individuals after aging (long-term comparisons) 1) a decrease in the total nightly sleep duration, 2) an increase in the number of nightly awakenings (sleep fragmentation), 3) a decrease in the mean sleep-bout duration (used as a proxy for the depth of sleep), and 4) an increase in the

mean awake-bout duration (time spent awake after sleep disruption).

4.2 Methods

4.2.1 Subjects and Site

We observed chimpanzees living at Kumamoto Sanctuary (previously named Chimpanzee Sanctuary Uto, a former laboratory facility) in Kumamoto, Japan. All individuals (N = 12) were males aged 23 to an estimated 48 (± 1) years at the time of data collection (October 2018–May 2019; Table 4.1). In the earlier study, which took place between October 2007 and April 2008, these same individuals were around 11 years younger, aged 12 to an estimated 37 (± 1) years (Morimura et al. 2012). During the day the chimpanzees lived in three all-male groups. Group composition changed daily, and chimpanzees had access to one of three outdoor enclosures of either 413 m^3 (W: 8.5 m, D: 12.8 m, H: 3.8 m, two enclosures) or 486 m^3 (W: 10.0 m, D: 12.8 m, H: 3.8 m, one enclosure) in area. One day every two weeks the three outdoor enclosures and a 150 m long corridor were open for all males to interact, if they chose to do so. Keepers separated individuals into individual indoor night rooms, each 10.8 m^3 in area (W: 2.0 m, D: 2.0 m, H: 2.7 m), before giving them dinner. While the chimpanzees remained socially isolated each night from the evening until the following morning (16:00 h to around 08:00 h), they were able to communicate with neighboring individuals visually and physically through a small section of iron bars. Indoor rooms were brightened by automatic lights set from 07:00 h to 19:00 h providing a light–dark condition of 12:12 each day, in addition to daylight reaching each night room through ceiling windows. While rooms were temperature controlled to 20–28 °C, outside air reached the rooms through a small gap in the door so outdoor seasonal changes may have slightly affected indoor conditions.

Previous studies have typically classified chimpanzees as “aged”, “old” or “elderly” from 30 or 33 years (e.g. Baker 2000; Videan 2006), but recently this boundary was increased to 35 and 37 years (Neal Webb et al. 2019; Hopkins et al. 2020). We classified chimpanzees aged 36 years or older as “old” adults because individuals in our study fell into two clear groups based on age; the oldest “prime” adult was 31 years of age (Table 4.1).

4.2.2 Data Collection

We recorded the chimpanzees’ nocturnal activity during 4 months (October 13–November 24, 2018, April 17–May 2, 2019) using a custom-built apparatus attached securely to the top of indoor night enclosures. We used infrared night vision cameras (Wyze Cam V2 1080p; Wyze Labs, Inc.) which we installed and maintained daily, rotating between two and six rooms per night. For the entirety of an individual’s night activity to be visible, one camera and one external infrared light (F8150_940nm; EnergyPower, Inc.) were required per room, placed on the center of the enclosure top and pointing down thus providing a “bird’s-eye view” (Fig. 4.1). In total we collected 123 recorded nights; of these we analyzed six per individual (72 in total) and compared our data with data from the 72 nights in Morimura et al.’s (2012) study.

Following Morimura et al. (2012), we used instantaneous sampling at 1-min intervals throughout the 13-h period (17:00–06:00 h) to record sleep. We defined sleep using behavioral criteria: a completely inactive posture with the body lying down and head on the floor or nesting materials. If an individual was in the same state (i.e., asleep or awake) at two consecutive time points, we assumed that they were in that state for the intervening period. Thus “sleep” as defined here may not have always been true sleep (i.e. the behavior we observed may not always have been

accompanied by the full physiological manifestation of sleep, especially sleep bouts of shorter durations). To identify sleep states precisely and non-invasively, allowing a thorough understanding of sleep architecture, requires techniques such as scoring behavioral signatures (e.g. respiration, random eye movement, Samson and Shumaker 2013), which was not possible in this study.

We generated descriptive statistics of four variables for each individual each night: 1) *total sleep duration* was the sum of all sleep bouts for each 13-h observation period, 2) *number of awakenings* was the count of all awake bouts occurring between sleep bouts, 3) *mean sleep bout duration* and 4) *mean awake bout duration*. We report means in the text for comparison with previous studies, although not all data were normally distributed and so we also provide medians and plot the data. We generated these variables, for both our data and for the data from Morimura et al. (2012), in two different ways: the first including all 1-min sampled data, which we term *high resolution* sleep, and the second considering only sleep bouts greater than 5 minutes in duration which we call *no tossing-turning* sleep. We used 5 sequential minutes of complete inactivity because the number of sleep bouts less than 5 minutes was highly skewed and following Videan (2006). Although a 1-minute awake bout may have more accurately identified an individual as truly awake (e.g. sitting up or standing to urinate in the night), it is unlikely that "true" sleep occurred during sleep bouts of only 1–4 minutes. Due to our use of infrared videography, rather than polysomnography or actigraphy, we could not be sure whether an individual entered actual sleep in any sleep bout, especially bouts of short duration, so we removed some of the noise present in the *high resolution* sleep data by using *no tossing-turning* data for some analyses.

Whereas Morimura et al. (2012) reported the maximum duration of sleep and awake bouts, we report their mean durations, due to potential variability across nights (e.g. a disruption from a

neighboring chimpanzee could result in a particularly long awake bout). We did not consider the effect of day length or external temperature on sleep behaviors because Morimura et al. (2012) found no effect of these variables and because indoor night rooms were on a time-controlled light and temperature setting.

4.2.3 Statistical Analysis

We used R to conduct statistical analyses (R Core Team 2017). To examine inter-individual variability in sleep patterns, we compared the four dependent sleep variables across individuals (2018–19 data only) using Kruskal–Wallis tests due to violations of the assumptions of the one-way analysis of variance (ANOVA), followed by Bonferroni *post hoc* tests. To examine the relationship between age category and sleep variables cross-sectionally (2018–19 data only), we ran a Welch two-sample t-test for *number of awakenings* (data normally distributed and variances homogeneous) and two-sample Wilcoxon rank tests with continuity correction for the other three variables. We used Welch two-sample t-tests to compare intra-individual changes between 2007–08 and 2018–19 data.

To perform linear mixed effects analyses of the relationship between age and the four sleep variables, we used the *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2016) packages. The data for *number of awakenings* was count rather than continuous so we used a Poisson generalized linear mixed model. We entered age as a fixed effect (we subtracted the minimum age from all ages), and as random effects we included intercepts for individuals to control for repeated measures (i.e. a random intercept model) and by-individual random slopes for the effect of age to allow individuals to show differing slopes. We used the *summary* function in R to compare the null (intercept only) models with the full models (Pinheiro and Bates 2000). We considered values

of $P < 0.05$ to be statistically significant, and report fixed-effects estimates and confidence intervals.

4.2.4 Ethical Note

For this study, we implemented no changes apart from installing cameras above six of the indoor night rooms. Food and water were available *ad libitum*. The care and study of the chimpanzees complied with the Guide for Animal Research Ethics provided by the Wildlife Research Center, Kyoto University and the Guide for the Care and Use of Great Apes of Kumamoto Sanctuary. The study was conducted in a manner commensurate with the ethical policy of the Wildlife Research Center, Kyoto University, as well as domestic and international laws related to the welfare and management of animals, and was approved by the Institutional Animal Experimentation Committee (#WRC-2018KS004A). The authors declare that they have no conflict of interest.

4.2.5 Data Availability

The data sets analyzed in the current study are available from the corresponding author on reasonable request.

4.3 Results

4.3.1 Sleep characteristics and cross-sectional comparison (2018–19 data only)

Twelve male captive chimpanzees, ranging from 23 to an estimated 48 years old in 2018–19, slept for a nightly mean duration of 10.5 ± SD 1.8 hours, or 631.6 ± SD 108.5 minutes, and showed individual differences (Kruskal–Wallis test: $H = 42.98$, $df = 11$, $P < 0.001$; Table 4.2). The

oldest individual, Lennon, slept a mean of 744 min (12.4 h) each night, the longest of all individuals, whereas Mizuo slept 492 min (8.2 h) per night. Shirou and George were the only two other individuals who slept less than 10 h per night. Chimpanzees experienced a mean of 15.1 ± SD 3.6 awakenings each night, and this also differed across individuals ($H = 31.13$, $df = 11$, $P = 0.001$; Table 4.2). Whereas Lennon woke up 11 times per night, Naoya woke up 20 times and had the most fragmented sleep.

The mean sleep bout duration was 45.4 ± SD 16.8 min and differed among chimpanzees (Kruskal–Wallis test: $H = 31.48$, $df = 11$, $P < 0.001$; Table 4.2). Naoya exhibited the shortest mean sleep bout, 33 min, whereas Lennon slept 40 min longer (73 min) per bout. The mean awake bout duration was 10.2 ± SD 8.2 min and also differed among individuals ($H = 37.38$, $df = 11$, $P < 0.001$; Table 4.2). Lennon experienced the shortest mean awake bout (4 min) and Shirou the longest (22 min). The mean of the maximum sleep bouts was 120 min (2 h); Mizuo experienced the shortest maximum sleep bout of 103 min (1.7 h) and Takaboh the longest of 288 min (4.8 h). The mean maximum awake bout was 50 min; George once stayed awake for 252 min (4.2 h) whereas Takaboh's longest period awake was 29 min.

We found no significant differences between "prime" and "old" adults in any of the four measured sleep variables: *total sleep duration* (Wilcoxon rank-sum test: $W = 582.5$, $P = 0.591$; Fig. 4.2a); *number of awakenings* (Welch two-sample t-test: $t = -0.590$, $P = 0.557$; Fig. 4.2b); *mean sleep bout duration* (Wilcoxon rank-sum test: $W = 589.5$, $P = 0.648$; Fig. 4.2c); *mean awake bout duration* (Wilcoxon rank-sum test: $W = 563$, $P = 0.448$; Fig. 4.2d).

4.3.2 Long-term comparison (2007–08 and 2018–19 data)

Nine individuals exhibited a significant change in at least one of the sleep measures across

the 11-year period, whereas three individuals (Mizuo, Shirou, Takaboh) showed no significant changes in any of the four variables (Fig. 4.3a–d and Electronic Supplementary Material Table 4.S1). As chimpanzees aged they experienced significantly more frequent awakenings (Table 4.3, Fig. 4.3b) and shorter sleep bouts (Table 4.3, Fig. 4.3c), so overall more fragmented sleep. Overall, the mean number of awakenings in 2007–08 was 11.6 ± SD 3.8 and increased to 15.1 ± SD 3.4 in 2018–19, and mean sleep bout duration decreased from 64.9 ± SD 27.8 to 45.4 ± SD 16.8 min (Table 4.2).

Neither total nightly sleep duration (Table 4.3, Fig. 4.3a) nor the length of awake bouts (Table 4.3, Fig. 4.3d) differed significantly between the two study periods after chimpanzees aged. Overall, the mean total sleep duration in 2007–08 was 670 ± SD 91.5 min (11.2 ± SD 1.5 h) and decreased to 632 ± SD 108 min (10.5 ± SD 1.8 h) in 2018–19, and mean awake bout duration showed little change from 9.9 ± SD 8.6 to 10.2 ± SD 8.2 min (Table 4.2). When we included only chimpanzees who transitioned from "prime" to "old" age between the two periods (N = 6; Table 4.1) in the model, there was again no significant relationship between age and total sleep duration (LMM: $\chi2 = 3.524$, df = 6, P = 0.060) or mean awake bout duration (LMM: $\chi2 = 1.072$, df = 6, P = 0.300), whereas the number of awakenings (GLMM: $\chi2 = 6.307$, df = 5, P = 0.012) and mean sleep bout duration again showed a significant relationship with age (LMM: $\chi2 = 7.647$, df = 6, P = 0.006).

4.4 Discussion

4.4.1 Sleep characteristics

The 12 adult male captive chimpanzees in the current study, all of whom were included in Morimura et al.'s (2012) study, slept a mean of 10.5 hours per night. Variation in sleep time has

been reported across captive chimpanzee groups, from a mean of 8.8 to 11.3 nightly hours (non-invasive studies only, Morimura et al. 2012; Videan 2006), and our findings fall within this range. Across populations, humans also show variation in sleep duration from as little as a mean 5.5 hours of sleep per night among Himba Namibian agropastoralists (Prall et al. 2018) to 7.9 hours per night among Melanesian horticulturalists (Smit et al. 2019). For a wider primate comparison, captive orangutans (*Pongo* spp.) slept a nightly mean of 9.3 hours and captive baboons (*Papio papio*) slept a nightly mean of 7.3 hours (Samson and Shumaker 2015).

Similar to what has been observed in the wild (Zamma 2014), chimpanzees in our study often woke up to defecate, urinate, drink, or adjust their posture or sleeping location due to the vocalizations of other individuals or for other reasons. They experienced a mean of 15 awakenings per night, considerably more than the three to five awakenings reported in a different group of captive chimpanzees, although in that study awake bouts were counted from a minimum of 2 minutes instead of 1 minute as in the current study (Videan 2006). Fifteen nightly awakenings was also more frequent than the 12 previously reported in Morimura et al. (2012), but nearly the same as orangutans who woke up a mean of 14 times per night, and less frequent than baboons who woke up 18 times (Samson and Shumaker 2015).

The mean nightly sleep bout duration, or period of undisturbed rest, may partly characterize the depth of sleep obtained. The mean sleep bout duration of the 12 chimpanzees was 45 minutes and the mean maximum sleep bout each night was 120 minutes. Chimpanzees' sleep bouts may be considerably shorter than humans', who typically spend 70 to 100 minutes in their first NREM-REM sleep cycle with subsequent cycles lasting longer (Institute of Medicine 2006). The mean awake bout duration of the chimpanzees was 10 minutes (awake bouts were most often only a single minute) and the mean maximum awake bout each night was 50 minutes. Because individuals

were physically separated throughout the night, there may have been fewer engagements or opportunities to keep them awake for as long as the mean 20 minutes reported in a captive group where chimpanzees remained together with indoor and outdoor access throughout the night (Videan 2006). One individual who stood out in our data was George, whose habit of licking his lips sometimes appeared to prevent him from falling asleep (maximum of 252 min), although once asleep he stopped engaging in this behavior. Our continuous data were non-normal, and data for similar variables in other studies may also not be normal; in such cases we recommend reporting medians in future work.

Similar to Morimura et al. (2012), we found high intra- and inter-individual variability in sleep patterns in chimpanzees, illustrating that repeated measures and several individuals are required for to characterize sleep in chimpanzees. This is likely the case for other primates as well. Our data suggested that the oldest individual included in our study, 48-year-old Lennon, experienced higher-quality sleep than most other individuals as he showed longer total sleep, fewer awakenings, longer sleep bouts and shorter awake bouts. Thirty-year-old Mizuo, by contrast, showed the opposite patterns. Three individuals, Mizuo, Shirou, and Takaboh showed highly consistent sleep patterns across the 11-year period, with no significant changes across any of the four sleep measures, whereas the other nine experienced significant changes. Mizuo and Shirou exhibited poorer sleep quality than most other individuals during both observation periods.

4.4.2 Cross-sectional comparison

In a cross-sectional comparison using only data from 2018–2019, we hypothesized that old chimpanzees (≥ 36 years, N = 7) would experience lower sleep quality than young adults (23–31 years, N = 5). However, we found no age-related significant differences across any of the four

measured sleep variables. Our findings contrast with the only other study comparing sleep between age classes, where old chimpanzees (N = 10) slept more and woke less frequently than prime adult individuals (N = 10), suggesting that they experienced higher quality of sleep (Videan 2006). The relatively small sample size may have influenced results in both studies, especially in light of the high inter-individual variation observed.

4.4.3 Long-term comparison

One of our aims was to re-assess the sleep of the same individuals living under the same conditions 11 years after Morimura et al. (2012; videos recorded in 2007–08). We hypothesized that as chimpanzees aged, they would experience lower sleep quality. Similar to the poorer quality of sleep observed among aging humans (e.g. Mander et al. 2017; Vitiello 2006), we found that as chimpanzees aged, they experienced more frequent awakenings and shorter sleep bouts. Greater disruption in sleep continuity may have contributed to the shortening of sleep bouts, which could suggest that individuals obtained less deep sleep at an older age. The sleep-wake cycle of mammals is partly regulated by circadian rhythms and homeostatic processes, along with environmental and various other factors, which change with increasing age and may influence sleep patterns in similar ways across species (Froy 2011; Gulia and Kumar 2018; Vitiello 2006). Humans and their ape relatives share other late-life changes, for example cardiovascular disease and other medical illnesses, which have been linked to decreases in human sleep quality (Doane et al. 2006; Vitiello 2006; Videan et al. 2009). Re-analyzing sleep data in light of health outcomes and survivorship of chimpanzees could reveal whether similar relationships are to be found in humans' nearest evolutionary neighbors.

In contrast to humans (e.g. Mander et al. 2017; Vitiello 2006), the effect of increasing age

on the chimpanzees' total nightly sleep duration and the duration of their awake bouts was variable and non-significant. Overall, chimpanzees did not significantly lose or gain sleep in older age, and they did not stay awake longer after awakening (e.g. to urinate, change position). One explanation for this may be simply that chimpanzees do not experience all of the same changes as humans as they age. Another explanation may be that because these chimpanzees were separated each night with little to do other than sleeping or resting, a decrease in total sleep and increase in awake bout duration was not observed.

Although we found no evidence of a population-level trend in changes in sleep quality as a function of age in the cross-sectional data, long-term data revealed decreasing quality in some sleep variables within individuals. However, five individuals were still prime-aged adults at the end of this study and thus not all individuals had reached "old" age. The precise time course of sleep changes in humans is not well established. Although it is often stated that as age increases, sleep quality decreases (e.g. Floyd et al. 2000; Gulia and Kumar 2018), a review concluded that most changes in humans' sleep occur during early and middle adulthood (age 19 to 60 years), whereas fewer changes occur in old age (60+ years) (Vitiello 2006). When we considered only chimpanzees who transitioned from "prime" to "old" age between the two time periods (N = 6) in analyses, the results were similar to those including all individuals, although they showed slight differences such as less nightly sleep. In summary, results from our long-term data showed that adult chimpanzees experienced some changes which suggest a decrease in sleep quality as they aged by 11 years.

4.4.4 Limitations

Our study is a small step towards a better understanding of the potential effects of age on

sleep in great apes. Although the chimpanzees' caretakers, living conditions, and routines remained mostly consistent between the two study periods, factors other than age may have influenced sleep (e.g. social rank, stress level, daily events or changes), especially given our relatively small sample size which was limited to males. When possible, future studies should include females, especially because human males show greater sleep impairments in old age than females (Mander et al. 2017). Another shortcoming of our study is that our attempt to study age-related changes on sleep was not truly longitudinal, as individuals were not observed regularly over an extended period of time, but during two periods of time 11 years apart. Additionally, our data collection method was restricted to the use of non-invasive infrared video recording and so we could not describe sleep architecture because we did not use polysomnography or actigraphy techniques. However, direct observation allowed us to obtain nightly postural and other nocturnal behavioral data for future analyses.

The comparability of observations of sleep behaviors in a captive group of apes and those in the wild or more ecologically relevant environments is not clear. The only study directly comparing sleep in wild and captive primates, in a nocturnal species, suggests that such comparisons may not be useful due to ecological differences shaping this behavior (Reinhardt et al. 2019). However, it has also been argued that it is possible to obtain species-typical sleep durations from captive animals based on the consistency of sleep observed in humans across various environments, and phylogenetically consistent sleep patterns across species (Capellini et al. 2008; Nunn and Samson 2018). Still, captive animals receive plentiful and consistent food, live in spaces where temperature and other ambient conditions may be controlled, and experience daily routines unlike those living in natural habitats. Such conditions could allow captive individuals to allocate more time to sleep, which may also be less disturbed.

4.4.5 Welfare considerations

Primates, like many other animals, spend half of their lifetime sleeping and resting, yet sleep-related behavior is considerably understudied compared to their waking activities (Anderson et al. 2019). Caretakers, researchers and staff working in a captive setting should strive to provide the best possible care to animals throughout their life. We suggest that examining sleep is important for a fuller understanding of animal behavior; non-invasive studies are needed to draw appropriate conclusions of sleep physiology and behavior due to the pain, suffering and stress involved in invasive studies. Monitoring sleep may also identify individual preferences and behaviors which may not be evident during the day, but that might be useful for improving welfare (see Samson et al. 2015 for cost-effective technologies). Providing species-appropriate sleeping sites is critical to positive welfare (Brando and Buchanan-Smith 2018). One change derived from the current study is that after sharing a selection of videos with care staff, they decided to increase the number of washable burlap sacks provided as bedding each night, especially to individuals who clearly used them. Additional changes to enhance the welfare of animals living in various captive environments may emerge from more focused studies on sleep in more species, and future research should highlight sleep's role in health for captive primates. Failing to adequately address sleep behavior could be restricting our understanding of primate biology and behavior, as well as our ability to assess individual welfare needs.

4.5 Figures

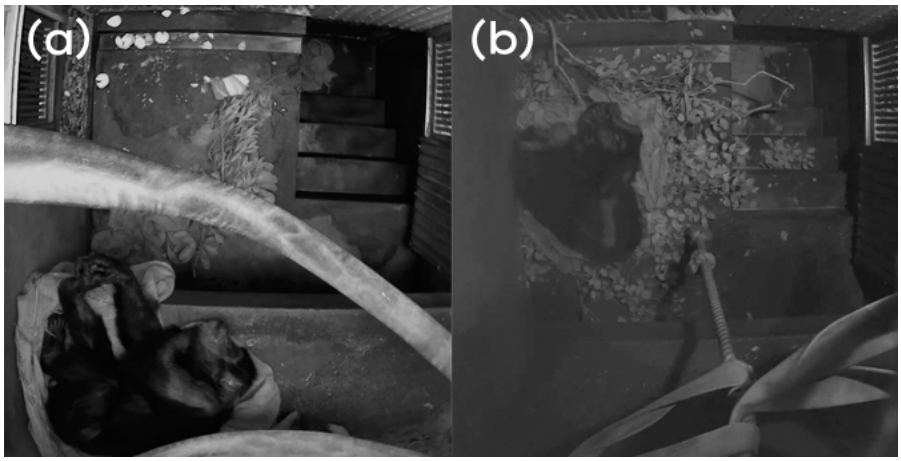

Fig. 4.1 Bird's eye views of chimpanzee Gorou sleeping at Kumamoto Sanctuary, Japan (a) Gorou sleeping on the upper platform of an indoor night room during the night of 20/04/2019; (b) Gorou sleeping on the floor on 23/11/2018.

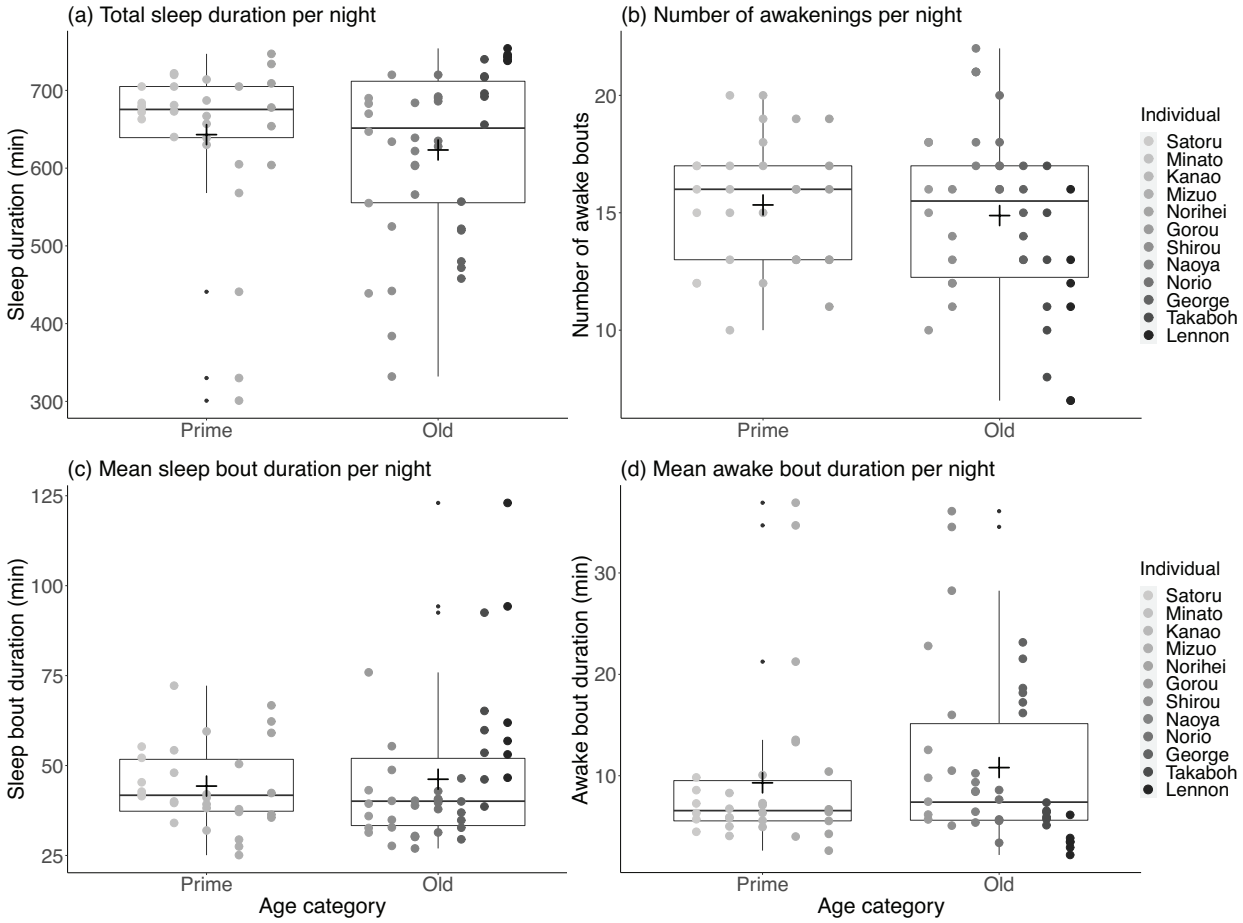

Fig. 4.2 Sleep patterns of 12 captive chimpanzees at Kumamoto Sanctuary, Japan by age category ("prime" and "old" adult) using 2018–19 data. Individuals are listed by age in ascending order in legend (left to right in boxplot). Boxplot lines represent the median value, crosses (+) display the mean, box edges are the interquartile range, and furthest points from the whiskers are the minimum and maximum values in the data.

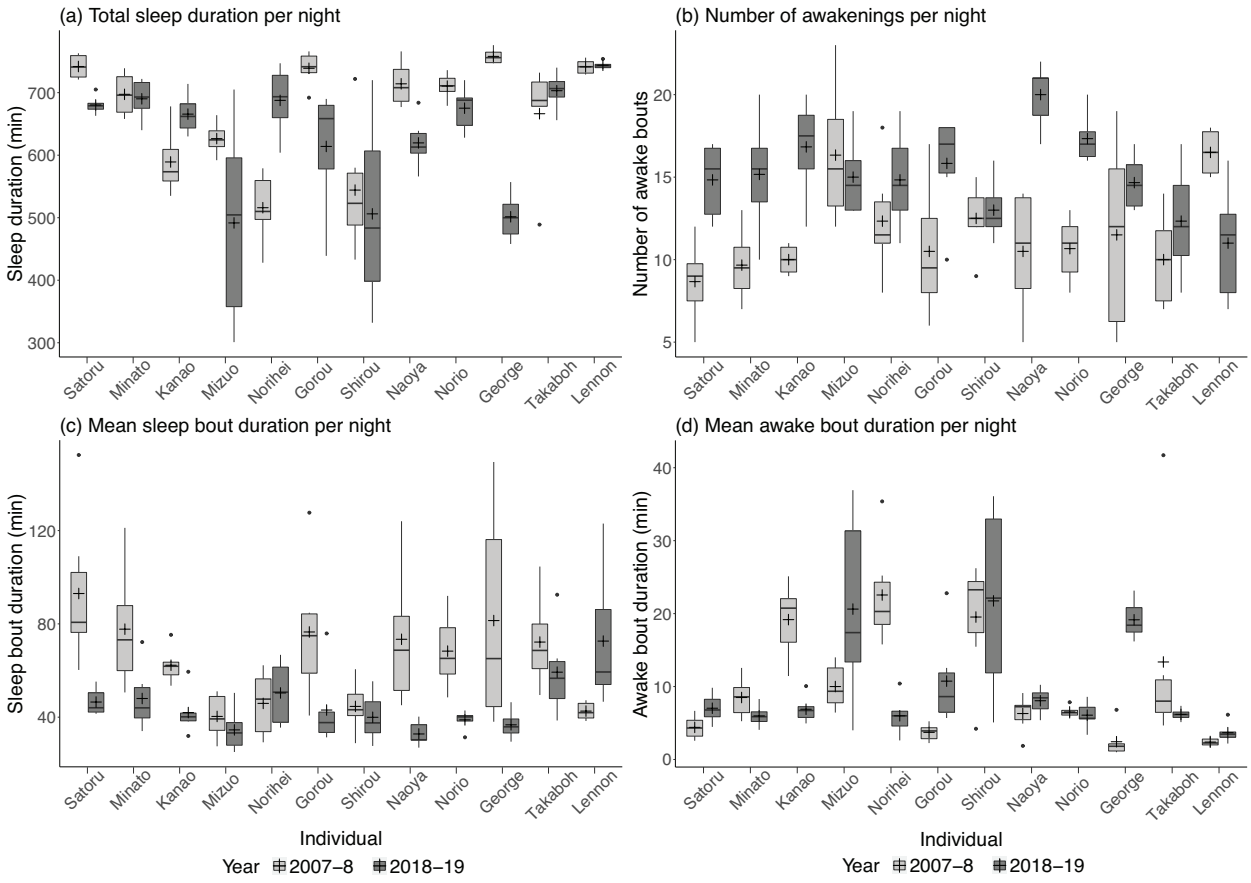

Fig. 4.3 Sleep patterns in 12 captive chimpanzees at Kumamoto Sanctuary, Japan in 2007–08 and 2018–19. Individuals are listed by age in ascending order from left to right. Boxplot lines represent the median value, crosses (+) display the mean, box edges are the interquartile range, and furthest points from the whiskers are the minimum and maximum values in the data.

4.6 Tables

Table 4.1 Description of captive chimpanzees at Kumamoto Sanctuary, Japan included in a study of sleep (2007–08, 2018–19). Age classes are prime-aged adults (P; 12–31 years) and old-aged adults (O; ≥ 36 years).

Individual	Birthplace	Year born	Age at start of first study (Oct 2007)	Age at start of current study (Sep 2018)	Age class at start of study	Age class at end of study
Satoru	Captivity	1995	12	23	P	P
Minato	Captivity	1992	15	26	P	P
Kanao	Captivity	1990	17	28	P	P
Mizuo	Captivity	1989	18	30	P	P
Norihei	Captivity	1987	20	31	P	P
Gorou	Unknown	e.1982	25	36	P	O
Shirou	Unknown	e.1982	25	36	P	O
Naoya	Wild	e.1981	26	37	P	O
Norio	Wild	e.1981	26	37	P	O
George	Wild	e.1979	28	39	P	O
Takaboh	Wild	e.1978	29	40	P	O
Lennon	Wild	e.1970	37	48	O	O

Table 4.2 Mean ± SD and [median (IQR)] of four sleep variables in 12 captive chimpanzees at Kumamoto Sanctuary, Japan (six nights per individual per period) for *high resolution* and *no tossing-turning* data (2007–08, 2018–19). *high resolution* data include all 1-min samples, whereas sleep bouts < 5 minutes were added to the previous awake bout in *no tossing-turning* data.

Data	Total sleep duration (min)	Total sleep duration (h)	Number of awakenings	Mean sleep bout duration (min)	Mean awake bout duration (min)
2018-19 *highres*	635.7 ± 108.2 [674.0 (101.5)]	10.6 ± 1.8 [11.2 (1.7)]	16.7 ± 3.9 [17.0 (5.0)]	41.2 ± 16.1 [37.2 (15.2)]	8.9 ± 7.3 [6.1 (5.4)]
2018-19 *notossing*	631.6 ± 108.5 [671.0 (101.3)]	10.5 ± 1.8 [11.2 (1.7)]	15.1 ± 3.4 [16.0 (4.0)]	45.4 ± 16.8 [40.4 (17.0)]	10.2 ± 8.2 [6.7 (4.9)]
2007-08 *highres*	673.7 ± 90.2 [706.5 (123.0)]	11.2 ± 1.5 [11.8 (2.1)]	13.1 ± 4.4 [13.5 (5.0)]	58.3 ± 28.1 [48.5 (27.6)]	8.2 ± 6.7 [6.0 (7.1)]
2007-08 *notossing*	670.4 ± 91.5 [704.0 (123.0)]	11.2 ± 1.5 [11.7 (2.1)]	11.6 ± 3.8 [11.0 (5.0)]	64.9 ± 27.8 [58.7 (31.9)]	9.9 ± 8.6 [6.8 (9.7)]
combined *highres*	654.7 ± 101.1 [683.0 (122.3)]	10.9 ± 1.7 [11.4 (2.0)]	14.9 ± 4.5 [15.0 (6.0)]	49.8 ± 24.4 [41.5 (21.0)]	8.6 ± 7.0 [6.1 (6.3)]
combined *notossing*	651.0 ± 101.9 [681.5 (122.3)]	10.9 ± 1.7 [11.4 (2.0)]	13.3 ± 4.0 [13.0 (5.3)]	55.1 ± 24.8 [48.3 (22.9)]	10.0 ± 8.4 [6.8 (7.6)]

Table 4.3 Results of linear mixed models investigating the influence of age on sleep variables in 12 captive chimpanzees at Kumamoto Sanctuary, Japan (2007–08, 2018–19).

Dependent variable	Predictor variables	Estimates	SE	*t* / *Z*	*P*
Total sleep duration (min)	Intercept	709.741	50.056	14.179 (*t*)	
	Age	-3.152	2.656	-1.186 (t)	0.259
Number of awakenings	Intercept	2.294	0.119	19.262 (*Z*)	
	Age	0.019	0.006	2.874 (*Z*)	0.004
Mean sleep bout duration (min)	Intercept	76.573	11.187	6.845 (t)	
	Age	-1.382	0.504	-2.744 (t)	0.018
Mean awake bout duration (min)	Intercept	-9.302	3.899	-2.386 (t)	
	Age	-0.008	0.214	-0.036 (t)	0.972

4.7 Supplementary Materials

Table 4.S1 Welch two sample t-test results for intra-individual comparisons between the two periods (2007–08 and 2018–19) across the four measured sleep variables of 12 captive chimpanzees at Kumamoto Sanctuary, Japan.

Sleep variable	Individual	Period (year) data was collected 2007–2008	2018–2019	*t*	R^2	*P*	Significance
Total sleep duration (min) mean ± SD [median (IQR)]	Satoru	741.8 ± 19.2 [741.0 (34.3)]	680.3 ± 14.1 [679.0 (9.5)]	-6.319	0.813	<0.001	***
	Minato	697.3 ± 35.4 [696.0 (56.8)]	690.2 ± 31.7 [693.0 (41.3)]	-0.369	0.014	0.720	
	Kanao	589.2 ± 51.9 [573.5 (50.5)]	665.7 ± 31.1 [662.0 (38.5)]	3.097	0.539	0.014	*
	Mizuo	626.5 ± 25.1 [624.5 (25.3)]	491.7 ± 160.8 [504.5 (238.0)]	-2.030	0.440	0.096	
	Norihei	516.0 ± 55.8 [510.0 (62.3)]	687.7 ± 53.6 [693.5 (67.8)]	5.436	0.747	<0.001	***
	Gorou	739.0 ± 27.0 [741.5 (26.5)]	614.0 ± 98.9 [658.5 (101.8)]	-2.988	0.609	0.026	*
	Shirou	544.2 ± 100.7 [523.0 (83.0)]	506.2 ± 149.5 [483.5 (208.3)]	-0.516	0.030	0.619	
	Naoya	714.2 ± 35.3 [708.0 (51.0)]	619.7 ± 39.8 [613.0 (31.5)]	-4.351	0.658	0.001	**
	Norio	710.5 ± 20.1 [711.0 (21.0)]	675.2 ± 36.0 [688.0 (43.8)]	-2.102	0.360	0.070	
	George	758.0 ± 11.7 [756.0 (16.8)]	501.5 ± 37.6 [500.0 (47.5)]	-15.953	0.977	<0.001	***

	Takaboh	666.3 ± 89.7 [687.5 (38.8)]	703.2 ± 28.9 [706.5 (24.8)]	0.957	0.132	0.375	
	Lennon	741.3 ± 11.3 [741.5 (18.3)]	743.8 ± 5.8 [743.0 (5.3)]	0.483	0.030	0.643	
Number of awakenings mean ± SD [median (IQR)]	Satoru	8.7 ± 2.4 [9.0 (2.3)]	14.8 ± 2.3 [15.5 (4.0)]	4.507	0.671	0.001	**
	Minato	9.7 ± 2.2 [9.5 (2.5)]	15.2 ± 3.4 [15.5 (3.3)]	3.323	0.567	0.010	**
	Kanao	10.0 ± 0.9 [10.0 (1.5)]	16.8 ± 2.9 [17.5 (3.3)]	5.469	0.835	0.002	*
	Mizuo	16.3 ± 4.2 [15.5 (5.3)]	15.0 ± 2.4 [14.5 (3.0)]	-0.674	0.053	0.519	
	Norihei	12.3 ± 3.4 [11.5 (2.5)]	14.8 ± 3.0 [14.5 (3.8)]	1.355	0.157	0.206	
	Gorou	10.5 ± 4.0 [9.5 (4.5)]	15.8 ± 3.1 [17.0 (2.8)]	2.559	0.410	0.030	*
	Shirou	12.5 ± 2.1 [12.5 (1.8)]	13.0 ± 1.8 [12.5 (1.8)]	0.447	0.020	0.665	
	Naoya	10.5 ± 3.7 [11.0 (5.5)]	20.0 ± 2.0 [21.0 (2.3)]	5.500	0.798	<0.001	***
	Norio	10.7 ± 2.0 [11.0 (2.8)]	17.3 ± 1.5 [17.0 (1.5)]	6.594	0.823	<0.001	***
	George	11.5 ± 5.8 [12.0 (9.3)]	14.7 ± 1.6 [14.5 (2.5)]	1.283	0.222	0.249	
	Takaboh	10.0 ± 2.8 [10.0 (4.3)]	12.3 ± 3.3 [12.0 (4.3)]	1.309	0.149	0.221	

	Lennon	16.5 ± 1.4 [16.5 (2.5)]	11.0 ± 3.5 [11.5 (4.8)]	-3.563	0.661	0.010	**
Mean sleep bout duration (min) mean ± SD [median (IQR)]	Satoru	93.0 ± 33.1 [80.7 (25.7)]	46.5 ± 5.8 [44.0 (8.3)]	-3.389	0.684	0.018	*
	Minato	77.7 ± 25.9 [73.2 (27.9)]	48.0 ± 13.8 [44.0 (13.0)]	-2.480	0.446	0.040	*
	Kanao	62.3 ± 7.5 [61.8 (5.4)]	42.0 ± 9.3 [40.1 (3.3)]	-4.170	0.645	0.002	**
	Mizuo	40.3 ± 9.6 [39.3 (14.5)]	34.6 ± 9.3 [33.3 (9.7)]	-1.055	0.100	0.316	
	Norihei	45.9 ± 13.9 [47.8 (22.6)]	50.4 ± 13.9 [50.7 (23.6)]	0.557	0.030	0.590	
	Gorou	76.5 ± 30.0 [74.9 (25.4)]	43.1 ± 16.7 [37.7 (8.7)]	-2.387	0.422	0.045	*
	Shirou	44.6 ± 10.7 [43.2 (9.1)]	40.0 ± 10.4 [37.5 (13.3)]	-0.763	0.055	0.463	
	Naoya	73.4 ± 29.4 [68.7 (31.8)]	32.8 ± 5.4 [30.3 (6.6)]	-3.330	0.675	0.019	*
	Norio	68.3 ± 16.1 [65.2 (19.9)]	38.9 ± 4.0 [40.1 (2.3)]	-4.340	0.771	0.006	**
	George	81.4 ± 47.3 [65.1 (71.6)]	36.7 ± 5.9 [35.9 (6.0)]	-2.297	0.506	0.068	
	Takaboh	72.2 ± 19.5 [68.6 (19.1)]	59.3 ± 18.8 [56.7 (15.9)]	-1.166	0.120	0.271	
	Lennon	42.6 ± 3.8 [41.9 (6.3)]	72.6 ± 29.8 [59.4 (32.2)]	2.450	0.538	0.056	

Mean awake bout duration (min) mean ± SD [median (IQR)]	Satoru	4.4 ± 1.6 [4.3 (2.2)]	7.0 ± 2.0 [6.8 (2.4)]	2.562	0.407	0.029	*
	Minato	8.5 ± 2.7 [8.6 (3.4)]	6.0 ± 1.5 [5.9 (1.3)]	-2.000	0.344	0.082	
	Kanao	19.2 ± 5.1 [20.8 (6.0)]	6.9 ± 1.8 [6.7 (1.5)]	-5.550	0.832	0.001	**
	Mizuo	10.0 ± 3.1 [9.4 (4.8)]	20.6 ± 13.0 [17.4 (18.0)]	1.946	0.404	0.103	
	Norihei	22.6 ± 7.0 [20.3 (5.8)]	6.0 ± 2.6 [6.0 (2.0)]	-5.389	0.820	0.001	**
	Gorou	3.7 ± 1.2 [3.9 (1.5)]	10.7 ± 6.4 [8.6 (5.4)]	2.632	0.566	0.044	*
	Shirou	19.5 ± 8.4 [23.3 (7.0)]	21.7 ± 13.0 [22.1 (21.1)]	0.350	0.014	0.735	
	Naoya	6.3 ± 2.5 [7.2 (2.0)]	8.1 ± 1.8 [8.5 (2.2)]	1.375	0.173	0.202	
	Norio	6.5 ± 0.8 [6.4 (0.6)]	6.1 ± 1.8 [5.6 (1.6)]	-0.546	0.042	0.603	
	George	2.4 ± 2.2 [1.8 (1.0)]	19.2 ± 2.7 [18.4 (3.3)]	11.875	0.936	<0.001	***
	Takaboh	13.4 ± 14.1 [8.0 (4.5)]	6.2 ± 0.8 [6.2 (0.7)]	-1.249	0.237	0.267	
	Lennon	2.4 ± 0.6 [2.3 (0.8)]	3.7 ± 1.3 [3.5 (0.7)]	2.146	0.398	0.069	

P<0.05 *, *P*<0.01 **, *P*<0.001 ***

Chapter 5

General Discussion

This research revealed the life history patterns of captive chimpanzees in Japan for the first time, describing female and male longevity estimates and mortality risks across all stages of life. Furthermore, it used these data to compare the survival patterns of the historical population of chimpanzees in Japan to those in America. Additionally, it explored whether chimpanzees experience behavioral changes as they age, specifically in their sleep patterns.

Detailed information on the life history patterns of chimpanzees is crucial in order to obtain a full understanding of their biology and has applications for captive welfare and population management. Despite this, only small and outdated captive chimpanzee life tables existed (Courtney & Santow 1989; Dyke et al. 1995; Littleton 2005). In addition to this, while the demographic composition and status of chimpanzees in Japan had been previously reported in Japanese (Watanuki et al. 2014; Ochiai et al. 2015), longevity and mortality statistics had not. In Chapter 2, the most up-to-date and robust captive chimpanzee life table was presented by single year of age and sex including 821 individuals and spanning nearly a century, using the Great Ape Information Network (GAIN). This showed that female and male survivorship did not differ significantly, and that a live-born chimpanzee in Japan could expect to live 28.3 years. Life expectancy increased to 34.6 years for individuals surviving beyond one year of age and to 40.4 years for those who reached adulthood. The oldest chimpanzee in Japan, a wild-born male, lived an estimated 68 years. Findings pointed to a high infant mortality rate as one in six individuals are stillborn and nearly 80% of all infants born alive survive beyond their first birthday. Also, it was discovered that a seasonal death pattern exists and that chimpanzees in Japan are more likely

to decease in the winter months (Dec-Feb) than in any other season. Together, the results from Chapter 2 provide foundational information which broaden our understanding of captive chimpanzee life history patterns and can be used for future captive management and welfare planning in Japan and around the world. Additionally, these life tables are crucial resources accessible for future comparative investigations into animal life history patterns.

Multi-regional comparisons of the survival patterns of captive animal populations are important as they can provide unique insights into why differences among the same species may exist. However, the opportunity to do this is limited due to the lack of access to long-term data typically held privately by zoos or in studbooks. In Chapter 3, the individual life history data of chimpanzees in Japan and America were used in a collaborative effort to describe their mortality rates and longevity estimates with the largest sample size to date and spanning more than four decades, as well as to explore whether significant differences existed between the two populations. Overall, similar survival patterns were found for both regional populations, such as the survival rates from infancy to old age, and birth type did not influence survival. Compared to a wild population, captive chimpanzees experience higher survival probabilities across their lifespan, with a median life expectancy of 35.7 years for females and 30.1 years for males from birth when both populations are combined. While females in America significantly outlive males, in Japan there was no significant difference between the sexes, consistent with findings from Chapter 2. Additionally, the seasonal death pattern revealed in Chapter 2 and re-confirmed in this study was not found in the American population. Chapter 3 results point to the necessity of further investigation into the varying captive conditions and management strategies at captive facilities across Japan, as well as in America, in order to better understand why these differences exist. As animals continue to age in each population and many have yet to live out their full

lives, future replication studies may explore whether life expectancy estimates increase as the quality of captive care improves over time.

Chimpanzees are one of many captive species of animals whose populations are rapidly aging across the world. To provide the best quality of care to aging individuals, it is crucial that we understand not only their survival patterns but also the physical, cognitive and behavioral changes they may experience as they grow old. Sleep is an activity which takes up a large portion of the lives of mammals, and diurnal primates spend around half of their lifetime sleeping or inactive. These nocturnal behaviors are considerably understudied compared to daytime activities. While it is well established that sleep quality diminishes with age in humans (e.g. Mander et al. 2017; Li et al. 2018), little is known about the effects of aging on sleep in our closest primate relatives. This has been difficult to study in primates due to the lack of research focus and longitudinal data. Chapter 4 described the sleep patterns of a group of captive chimpanzees and was the first study to use longitudinal data to examine whether individual sleep quality changed over a decade period. Results indicate that chimpanzees slept 10.5 hours and woke up 15.1 times on average each night. Sleep patterns varied greatly, illustrating that large individual variation exists. As chimpanzees aged, they experienced significantly more frequent awakenings and shorter sleep bouts (i.e. more fragmented sleep), similar to findings from human studies. Thus, results from Chapter 4 shed light into why humans age the way we do, suggesting that the decrease in sleep quality humans' experience may not be due to modern day adaptions, but may be a behavioral change with aging that has existed since at least the time of the chimpanzee and human evolutionary split. The finding that chimpanzees' sleep patterns change as they age will be important to take into consideration for future captive care and welfare

planning, and adds to the currently sparse literature on behavioral changes that occur with aging in non-human primates.

Chimpanzees are the closest living evolutionary relatives of humans, along with bonobos, and thus studying the life history patterns and behaviors of primates can reveal important insights not only about them, but also into the evolution of human traits and behaviors. The detailed life history patterns, including longevity estimates and mortality rates, of various captive species remains unknown. Prior to this research, previously published life tables of captive chimpanzees did not contain individuals old enough or in large enough numbers to accurately predict their longevity patterns. Without this information, future captive animal management planning is difficult, if not impossible. For example, it is not possible to make reliable predictions of future populations' demographic composition and size without knowledge about infant mortality and lifespan estimates. In addition to this, reports on the life history patterns of primates other than chimpanzees, including robust life tables, are necessary for future cross-species comparative investigations. Various studies have explored the similarities and differences between chimpanzee and human life history patterns (e.g. Thompson et al., 2007; Hawkes et al. 2009; Wood et al., 2017; Davison & Gurven, 2021). Life expectancy at birth for hunter-gatherers ranges from 21-37 years across groups and on average 35% of people survive to age 45 (Gurven & Kaplan, 2007), similar to what has been found in a wild (Wood et al., 2017) and a captive chimpanzee population (Chapter 2; Havercamp et al., 2019). Although, wild chimpanzees typically live less long than their captive counterparts (Chapter 3; Che-Castaldo et al., 2021). Studbooks are a robust and valuable resource that can be used to investigate and compare the life history patterns of animals, especially at this time as captive populations around the world have existed for decades and a portion of these animals have reached or are reaching their maximum

longevity. Future life history pattern comparisons across different captive populations, not only among chimpanzees (Chapter 3), may expose similarities or differences in survival patterns which could be further examined for determining best management strategies such as husbandry techniques, diet and veterinary care. To proceed with such research, further collaboration is required between zoos, researchers and across countries.

Various changes that occur with aging have been described in chimpanzees. Physical changes such as an increase in cortisol levels (Emery Thompson et al. 2020a) and moderate declines in physical condition (Emery Thompson et al. 2020b) have been discovered, reflecting human aging processes. Cross-sectional and longitudinal age-related cognitive decline in chimpanzees have also been exposed (Hopkins et al. 2021). While some changes in behavior have been reported such as increasing social selectivity (Rosati et al. 2020) and decreased aggression (Baker 2000), there has been less focus on behavioral aspects of aging not only for chimpanzees, but for many animals in general. The finding that chimpanzee sleep quality decreases as they age, similar to humans (Chapter 4; Havercamp et al., 2021), adds to this limited existing literature on behavioral aging. One of the main challenges to exploring behavioral changes with age is the lack of longitudinal data, especially for long-lived species. However, such data are important because exposing the various changes chimpanzees undergo with aging has the ability to shed light onto what we may consider "healthy" human aging, as there may be shared patterns which exist since our evolutionary split. Thus, attention should be given to collecting long-term individual data in order to be able to focus on all aspects of aging including physical, cognitive and behavioral aging.

Various efforts are being made to improve the welfare of captive chimpanzees and other primates such as providing novel enrichment devices (e.g., painting with brush on paper or on a

digital tablet device: Grunauer & Walguarnery 2018; providing interactive art in the form of a virtual forest: Yamanashi et al. 2021), increasing positive social opportunities (e.g., offering social opportunities which reflect social grouping patterns in the wild: Ross et al. 2009; integrating caregivers as meaningful social partners: Funkhouser et al. 2021), to performing innovative treatments for the improvement of physical alignments that can occur with natural aging (e.g., acupuncture as a form of therapy for osteoarthritis: Magden et al. 2013; providing self-medication opportunities for arthritis: Neal Webb et al. 2018). All such initiatives are in response to the more easily observable, daytime activities of chimpanzees. However, given that captive primates spend around half or more of their lives in night rooms or asleep, it is crucial that more effort is put onto improving this less visible time. This research highlights new avenues for future welfare considerations beyond the observable day time, suggesting that caretakers and/or researchers at zoos, sanctuaries and other facilities attempt to record the night rooms of chimpanzees and other primates if they are not doing so already. During the course of analyzing sleep videos (Chapter 4), diverse individual preferences in the use of bedding were discovered and the amount of burlap sacks provided each night was changed accordingly (i.e., bedding was increased for individuals who showed nest building behaviors or a general interest in using the sacks, which was unrelated to age). Failing to adequately address sleep behavior could be restricting our understanding of primate biology and behavior, as well as our ability to assess individual welfare needs, and future studies should highlight sleep's role in health for captive animals.

Animal aging is not only understood through their life history patterns, but also by the various changes they experience physically, cognitively and behaviorally. By combining life history data with information about behavioral changes that occur with aging in captive

chimpanzees, this research aims to provide a fuller understanding of their basic biology, life expectancy and behaviors, especially during a critical period of time as populations will soon consist of a majority elderly individuals. Data presented here will be valuable for future population management and welfare planning, as well as for comparative studies within and between species. As captive animal populations continue to age, future research should continue to investigate changes individuals undergo as well as re-analyze survival data on a population level in order to explore whether longevity and mortality rates are changing as the quality of captive care improves over time.

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