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Title: The Influence of Age and Sex on Measures of Body Size in  
Captive Chimpanzees (*Pan troglodytes*) Cared for in African Wildlife  
Sanctuaries and Zoological Collections

Offer for the Award of Master of Philosophy

Discipline: Comparative Physiology

Submission: 19<sup>th</sup> May 2020

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This research was undertaken under the auspices of Cardiff  
Metropolitan University.

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## **Acknowledgements**

Foremost, I would like to sincerely thank my Director of Studies Dr Mike Stembridge, and my supervisor Prof Rob Shave, for their continued guidance, expertise and support throughout my MPhil. I would also like to thank Ms Aimee Drane, who was an adviser to my supervisory team, for always being there and providing valuable advice. It has been an incredible experience to work with you all so closely and I have learnt a great deal.

In addition to my supervisory team, I would also like to thank all those that without whom, this research would not have been possible. I am incredibly grateful to all the members and friends of the International Primate Heart Project who organised and assisted with the chimpanzee health checks. I also have a tremendous appreciation to all the staff at Tchimpounga Wildlife Sanctuary, Chimfunshi Wildlife Sanctuary and Tacugama Chimpanzee Sanctuary that care for the sanctuary chimpanzees included in this study. Many thanks also to Species360 for the body mass data of chimpanzees housed in zoological facilities and to Meg Sleeper and Michael Lammey for sharing the body mass of the Alamogordo Primate Facility chimpanzees. I would also like to thank Prof Steve Cooper, for all his statistical advice.

Lastly, to my wonderful family and boyfriend, thank you for supporting and encouraging me every step of the way.

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## **Abstract**

**Introduction:** The typical growth pattern of chimpanzees (*Pan troglodytes*) has largely been derived from captive research populations, as methodological and ethical challenges limit assessment of their wild counterparts. Despite a lack of empirical evidence, captive research chimpanzees have been suggested to display accelerated growth compared to wild animals. Wild-born sanctuary chimpanzees may provide a more ecologically valid population from which to infer species-typical growth. The aim of this study was to investigate the growth pattern of male and female sanctuary chimpanzees and compare these data to animals in zoological and research facilities.

**Methods:** Body mass and crown-rump length were obtained from 150 male and 148 female (aged 1 - 38 years) African sanctuary chimpanzees. Sex-specific piecewise linear regressions were performed to estimate growth rates and age at maturation. Body mass regressions were compared to those of 454 male and 623 female chimpanzees (aged 1 - 40 years) acquired from a centralised zoological database. A literature search of peer-reviewed publications was conducted to identify body mass data of research facility populations, which were presented for comparison.

**Results:** Male sanctuary chimpanzees attain body mass maturation at an older age compared to females (13.8 vs 12.4 years), but sex differences were not observed in maturation age for crown-rump length or the growth rates for either measure. In comparison to zoological animals, sanctuary chimpanzees had a slower estimated rate of body mass growth and attained maturation at an older age (males: 13.8 vs. 12.2 years; females: 12.4 vs. 12.2 years). Sanctuary chimpanzees were also lighter than zoological (males: 53 vs. 61 kg; females: 44 vs. 52 kg) and research animals.

**Conclusion:** Together, these results suggest that growth patterns between African sanctuary, zoological and research facility populations of chimpanzees differ. These differences need to be considered when examining life history characteristics in this species. Additionally, these sanctuary data contribute significantly to current understanding of chimpanzee growth.

## 1. Introduction

The study of chimpanzee (*Pan troglodytes*) growth and maturation provides valuable insight into the species' life history and the trade-offs that occur during development (Hamada & Udono, 2006). Comprehensive studies of growth require either multiple measurements of the same animal to be collected longitudinally, or multiple animals of differing ages to be assessed at a single time point (Turner, Cramer, Nisbett, & Patrick Gray, 2016). Accordingly, the vast majority of studies in this area have been conducted using captive chimpanzees in research facilities, where numerous individuals of known chronological age have been assessed regularly (Gavan, 1953; Grether & Yerkes, 1940; Hamada & Udono, 2002; Hamada, Udono, Teramoto, & Hayasaka, 2004; Hamada, Udono, Teramoto, & Sugawara, 1996; Leigh, 1994a; Smith, Butler, & Pace, 1975; Watts & Gavan, 1982). In contrast, information regarding the growth of chimpanzees in zoological institutions is scarce (Behringer et al., 2016; Vancata & Vančatová, 2002). Furthermore, despite previous research in wild chimpanzees (Kimura & Hamada, 1996; Morbeck & Zihlman, 1989; Pusey, 1978; Pusey, Oehlert, Williams, & Goodall, 2005; Uehara & Nishida, 1987; Zihlman, Bolter, & Boesch, 2007; Zihlman, Morbeck, & Goodall, 1990), our understanding of growth and somatic maturation in this population remains limited. This is because many previous reports of body size in wild chimpanzees are from single case studies based on animals that were either shot for museum collections (Shea, 1981) or were deceased when found (Kimura & Hamada, 1996; Matsuzawa, Sakura, Kimura, Hamada, & Sugiyama, 1990; Morbeck & Zihlman, 1989; Zihlman et al., 2007; Zihlman et al., 1990). Often, the skeletal remains of deceased chimpanzees are of unknown age and/or sex (Kimura & Hamada, 1996; Morbeck & Zihlman, 1989; Uehara & Nishida, 1987; Zihlman et al., 2007) and based on the opportune nature of data collection, sample sizes are typically small (Kimura & Hamada, 1996; Matsuzawa et al., 1990; Uehara & Nishida, 1987; Zihlman et al., 2007; Zihlman et al., 1990). A notable exception to these case studies, however, are the chimpanzees of Gombe National Park, in which body mass has been assessed longitudinally (Pusey et al., 2005). Together, these data have been used to characterise the species' normative growth pattern for a multitude of research questions in biology.



### **1.1 Crown-Rump Length**

The development of body size is particularly useful for exploring and assessing the stages of somatic growth (Behringer et al., 2016). Crown-rump length is commonly used as a substitute for 'height' in primates (Hamada & Udono, 2006; Huck, Rotundo, & Fernandez-Duque, 2011; Kemnitz, Sladky, Flitsch, Pomerantz, & Goy, 1988; Raman et al., 2005), but few have reported this measure in chimpanzees (Coolidge & Shea, 1982; Hamada & Udono, 2006; Shea, 1981). To date, only one study has attempted to comprehensively characterise the growth of crown-rump length in this species. Hamada and Udono (2006) used cross-sectional data to generate an average growth curve which inferred that a sex-difference was noticeable from the age of 5.5 years, when males overtook females in stature. The maximum crown-rump lengths were reportedly attained at 13.8 years and 15.7 years of age in males and females, respectively, but the authors did not comment on the methodology used to calculate these ages (Hamada & Udono, 2006). Other studies have used alternative measurements of 'height' to assess body growth in research facility chimpanzees, including trunk length (Gavan, 1953; Hamada et al., 1996; Schoonaert, D'Aout, & Aerts, 2007) and the summation of trunk, thigh and leg lengths (Hamada & Udono, 2002). These studies observed no pronounced sex difference in size and reported that growth had plateaued by 12 years of age (Gavan, 1953; Hamada & Udono, 2002; Schoonaert et al., 2007).

Overall, there is currently limited literature regarding the growth and development of body size in chimpanzees. Further, owing to the ethical and methodological challenges of obtaining crown-rump length in wild animals, current literature is only based upon measurements taken in research facility chimpanzees (Gavan, 1953; Hamada & Udono, 2002, 2006; Hamada et al., 1996). Previous studies have assessed skeletal remains from the wild to gain an indication of body size in this population, but these studies typically only examine limb lengths (Kimura & Hamada, 1996; Morbeck & Zihlman, 1989; Zihlman et al., 2007; Zihlman et al., 1990). Additionally, interpretation and extrapolation of wild data is limited as the chimpanzees were often of unknown age and/or sex and the sample sizes were small (Kimura & Hamada, 1996; Morbeck & Zihlman, 1989; Zihlman et al., 2007; Zihlman et al., 1990). Nonetheless, data from the skeletons of wild chimpanzees would suggest that they have much shorter limbs (Kimura & Hamada, 1996; Morbeck & Zihlman, 1989) and mature later in limb length

compared to their captive counterparts (Kimura & Hamada, 1996; Zihlman et al., 2007). Zihlman et al. (2007) reported that skeletal maturation times may be extended by as much as three years in wild chimpanzees. Accordingly, it is possible that wild chimpanzees may also demonstrate a comparatively shorter crown-rump length and mature later than those in research facilities.

## **1.2 Body Mass**

### *1.2.1 The growth pattern*

Individual body mass can provide an easily accessible indicator of the overall health of an animal (Brent, 1995; Leigh, 1994b). While many studies have reported chimpanzee body mass as an incidental finding (Elliott et al., 2007; O'Neill, Umberger, Holowka, Larson, & Reiser, 2017; Pontzer, 2017; Robson & Wood, 2008; Seiler et al., 2009; Shave et al., 2019; Sleeper, Drobatz, Lee, & Lammey, 2014), there are comparatively fewer reports characterising the growth patterns of research facility (Gavan, 1953; Grether & Yerkes, 1940; Hamada et al., 1996; Leigh & Shea, 1996; Smith et al., 1975) and wild chimpanzees (Pusey et al., 2005). Nonetheless, it has been suggested that both sexes share a similar growth trajectory until approximately 7 – 10 years of age (Grether & Yerkes, 1940; Leigh & Shea, 1996; Pusey et al., 2005). At which point, males continue to grow rapidly whereas females experience a marked deceleration in body mass growth (Grether & Yerkes, 1940; Leigh & Shea, 1996; Pusey et al., 2005). Consequently, female chimpanzees are typically lighter and attain body mass maturation (i.e. asymptotic adult body mass) earlier than their male counterparts (Hamada et al., 1996; Pusey et al., 2005).

### *1.2.2 Social and environmental factors influencing body mass*

In the wild, chimpanzees live in complex social groups which adopt a dominance hierarchy (Funkhouser, Mayhew, & Mulcahy, 2018). High-ranking individuals have been reported to maintain a more stable body mass than that of low-ranking chimpanzees, suggesting competition over food is important in both sexes (Pusey et al., 2005). This is particularly true in females, where greater dominance is associated with increased body mass (Pusey et al., 2005). For example, within the Gombe community, the highest-ranking female was reported to be approximately 11% heavier than the lowest-ranking female (Pusey et al., 2005). Additionally, maternal rank has

been reported to influence the muscle mass of weaned offspring, whereby higher-ranking females have offspring with greater muscle mass (Samuni et al., 2020). However, it is currently unknown whether similar trends exist in captive chimpanzees housed in smaller contrived groupings, where food is likely to be evenly distributed between individuals. Furthermore, body mass has been shown to vary across seasons (Grether & Yerkes, 1940; Pusey et al., 2005). In both research facility and wild chimpanzees, body mass is greater during late autumn and winter compared to spring and summer (Grether & Yerkes, 1940; Pusey et al., 2005). Pusey et al. (2005) has suggested that, in wild chimpanzees, this pattern may be driven by rainfall which subsequently affects food availability. Chimpanzees housed in research facilities are unlikely to be affected by this, but their body mass may be influenced by the opportunity to be physically active. Grether and Yerkes (1940) note that during the colder months, there was reduced opportunity for activity as the animals did not have access to the outdoors.

It has also been suggested that the growth pattern of chimpanzees is influenced by the environment in which they live (Zihlman et al., 2007). Chimpanzees in research facilities appear to have a greater body mass than their wild counterparts (Brent, 1995; Hamada et al., 1996; Kimura & Hamada, 1996; Pusey, 1978), although no data explicitly examining this difference currently exists. Further, the tempo of growth appears to differ between living environments. Both Grether and Yerkes (1940) and Leigh and Shea (1996) reported that males started to become heavier than females at 7 – 8 years of age in research facilities; whereas, this sex difference did not occur until approximately 10 years of age in wild chimpanzees (Pusey et al., 2005). It is important to note, however, that the pattern of body mass growth has only been assessed in one community of wild chimpanzees (Pusey et al., 2005). Pusey et al. (2005) longitudinally assessed the body mass of 31 males and 26 females of Gombe National Park, but of these, only 19 males and 14 females were <12 years of age (immature) when weighed. This small sample size may be insufficient to provide information regarding the growth pattern of immature individuals and may also not be reflective of other wild populations.

The accelerated growth seemingly apparent in research facility chimpanzees results in body mass maturation occurring much earlier than those in the wild (Hamada et al., 1996). Estimated maturation ages of research facility populations vary, but typically

range between 12 - 15 years of age for males (Hamada et al., 1996; Leigh & Shea, 1996; Smith et al., 1975) and 11.5 – 12.5 years of age for females (Gavan, 1953; Hamada et al., 1996; Leigh & Shea, 1996). By contrast, male chimpanzees of Gombe National Park were estimated to have reached adult body mass at 15 years of age (Pusey, 1978). No current maturation age has been estimated for wild females, although Figure 4.2 from Pusey (1978) indicates that Gombe females reach a plateau in body mass at approximately 14 years of age.

### ***1.3 Explanations for the Proposed Captive-Wild Difference in Growth***

Notwithstanding the methodological issues with data in wild chimpanzees, differences appear to exist in the size and temporal pattern of growth between research facility and wild populations (Kimura & Hamada, 1996; Zihlman et al., 2007). Consequently, extrapolating life history characteristics and growth parameters from captive populations to free-ranging chimpanzees is problematic (Grether & Yerkes, 1940; Matsuzawa et al., 1990). Several explanations have been proposed as to why differences exist between the growth of captive and wild populations, but the influence of energy expenditure and food availability are the most commonly reported (Hamada & Udono, 2006; Zihlman et al., 2007).

#### ***1.3.1 Energy expenditure***

In the wild, chimpanzees have immediate access to large expanses of vegetation to roam and forage (Zihlman et al., 2007). Chimpanzees feed in multiple trees each day, requiring regular bouts of vertical climbing and arboreal travel (Pontzer & Wrangham, 2004). In between these feeding sessions, wild chimpanzees travel long distances on the ground; the daily average for adults is ~5 km (Pontzer & Wrangham, 2004), whereas juveniles of the Taï forest have been reported to travel a daily average of 4 – 11 km (Christophe Boesch & Boesch-Achermann, 2000). In addition to this daily energy expenditure, male chimpanzees also engage in large territorial border patrols, which reportedly occur approximately every 10 or so days (Amsler, 2010). The average patrol time for one community within Kibale National Park was 134 minutes and the distance covered can be more than 5 km per patrol (Amsler, 2010). Wild chimpanzees also hunt approximately 4 – 10 times each month (Mitani & Watts, 2001). C. Boesch and Boesch (1989) report a mean hunt time of 18.2 minutes for the Taï

chimpanzees, but the hunt can continue for up to two hours in duration. Subsequently, terrestrial travel accounts for the greatest percentage of daily energy expenditure in these wild animals (~10 - 15% of the total expenditure; Pontzer and Wrangham, 2006). Furthermore, wild chimpanzees live in large multi-male, multi-female fission-fusion communities with 20 – 150 members (Christophe Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1968). This complex social hierarchy is energetically demanding to navigate, and chimpanzees face greater competition for food resources than those in captivity (Zihlman et al., 2007).

Chimpanzees in captivity are likely to have comparatively lower energy demands than wild animals. In research facilities, the animals inhabit cages that confine them to an enclosed space (Wobber & Hare, 2011). Often, chimpanzees have outdoor access which typically provides a large space for exercise (Videan, Fritz, Schwandt, Smith, & Howell, 2005), but this access is not always continuously available; some animals have access every other day (Videan et al., 2005), some have seasonal access (Grether & Yerkes, 1940) and some do not have access at all (Videan et al., 2005). Further, many studies do not actually comment on the size of the cages, so it is hard to quantify exactly how much space these animals have for movement (Andrade et al., 2011; Smith et al., 1975; Videan et al., 2005). However, it is reasonable to assume that research facility chimpanzees do not travel the same daily distance as their wild counterparts, so likely have a comparatively reduced energy expenditure. There is also a lack of cognitive stimulation and foraging opportunities within research facilities, and predators are obviously absent (Celli, Tomonaga, Udono, Teramoto, & Nagano, 2003) which leads to general inactivity in these animals (Paquette & Prescott, 1988). The physical environment of research facilities further promotes inactivity as it is not as three-dimensionally complex as the wild; there are increased hard surfaces (e.g. concrete and stainless steel) and little variation in heights and inclines (Lewton, 2017). Additionally, cage conditions such as the climate are controlled (Bribiescas & Anestis, 2010; Zihlman et al., 2007) and so the chimpanzees do not need to devote energy for thermoregulation. Research facility animals are also often housed in small (usually between 2 – 7 individuals), same-sex groups (Andrade et al., 2011; Funkhouser et al., 2018; Videan et al., 2005). For these reasons, juvenile chimpanzees in research facilities are likely to have a surplus of energy available for growth, which may result in adiposity if not managed.

Zoological institutions differ from research facilities in that the chimpanzees are typically housed in exhibits that are more three-dimensionally complex and are much greater in size. Enclosures often have daily outdoor access (AZA Ape TAG, 2010), enabling the animal to move freely. Additionally, many zoological institutions provide objects for environmental enrichment which encourages activity of the chimpanzees (Paquette & Prescott, 1988). While zoological animals will typically have more space for physical activity than those in research facilities, they are still likely to have comparatively more energy available for growth than their wild counterparts. Additionally, chimpanzees in zoological institutions are typically housed in mixed-sex and mixed-age groups of a larger size than that found in research facilities (AZA Ape TAG, 2010), but this can vary. Birkett and Newton-Fisher (2011) observed a range in group size of 3 – 11 individuals across six accredited zoological institutions in the United Kingdom and United States of America, which is markedly smaller than that typically observed in wild populations.

### *1.3.2 Diet*

Growth and body size are greatly influenced by nutrition (Brent, 1995; Hamada et al., 1996) which differs significantly between chimpanzee living environments. Wild chimpanzees spend approximately 30 – 60% of their daily activity foraging for foods such as ripe fruit, which is a consistent primary food source (Kisidayova et al., 2009; Struck, Videan, Fritz, & Murphy, 2007; Yamakoshi, 1998). Other plant matter, such as leaves, pith, bark and herbaceous vegetation tend to comprise 25% of the diet (Struck et al., 2007; Yamakoshi, 1998), while foods such as termites, ants and vertebrae prey typically only make up 4 – 6% (Kisidayova et al., 2009). However, these proportions will vary with season as the availability of fruit fluctuates (Yamakoshi, 1998). By contrast, chimpanzees in research facilities and zoological institutions receive 2 – 3 discrete meals each day and are fed a diet of commercial primate biscuit (AZA Ape TAG, 2010). Captive animals are also supplemented with domesticated fruit and other foods as enrichment (Brent, 1995; Struck et al., 2007). This calorie-dense food is comparatively higher in simple sugars and lower in fiber than the diet of wild chimpanzees, and hence is often easier to digest (AZA Ape TAG, 2010; Kisidayova et al., 2009; Struck et al., 2007). In humans, research has established an association between diets that are high in fat and sugar with precocious puberty (Chen et al., 2018). Accordingly, a similar association may be present in chimpanzees, which could

contribute to the reported discrepancy in the timing of maturation between wild and captive populations. Furthermore, feeding practises during early life may also have implications for weight gain in chimpanzees. In research facilities, some infants will be removed from their mothers and will require bottle feeding, whereas wild chimpanzees will be breastfed. In humans, breastfed infants gain weight slower than formula-fed and have a lower risk of later childhood obesity (Li, Magadia, Fein, & Grummer-Strawn, 2012; Owen et al., 2005).

It has long been established that a surplus of nutrients without balanced physical activity will inevitably result in a deposition of fat (Hamada & Udono, 2006). Therefore, it is perhaps unsurprising that obesity has been an acknowledged health concern in captive chimpanzee populations for decades (Videan, Fritz, & Murphy, 2007). However, only a handful of studies have clearly defined obesity in this species (Nehete, Magden, Nehete, Hanley, & Abee, 2014; Videan et al., 2007). Nehete et al. (2014) assessed the body condition score of obese chimpanzees and defined individuals 'as having a very large abdomen that extends outside of body frame, pectoral fat, the presence of fat around gluteal muscles and fatty deposits in axillary regions and or/below biceps'. Whereas, Videan et al. (2007) defined obesity as a BMI > 20% above the mean for the population, and reported an average BMI of 141 kg/m<sup>2</sup> for overweight females (compared to 115 kg/m<sup>2</sup> for non-overweight females). Despite inconsistent definitions, unhealthy weight gain has been associated with a variety of co-morbidities in chimpanzees, including hypertension (Andrade et al., 2011; Ely, Zavaskis, & Lammey, 2013), insulin resistance (Andrade et al., 2011), cardiovascular disease (Seiler et al., 2009), metabolic syndrome (Nunamaker, Lee, & Lammey, 2012) and inflammatory disease (Nehete et al., 2014; Obanda, Omondi, & Chiyo, 2014).

### *1.3.3 Contraception and Castration*

In captivity, a variety of contraceptives are used in female chimpanzees to manage population size, including implants, intrauterine devices and oral contraceptive agents, which contain artificial progesterone or oestrogen and progesterone (Bourry, Peignot, & Rouquet, 2005; Gould & Johnson-Ward, 2000). Although minimal research has investigated the effect of contraceptives on chimpanzee growth, they are unlikely to have a direct effect on body mass or stature. Bourry et al. (2005) reported no difference in weight gain between implanted chimpanzees and ligated females, or between

females using intrauterine devices and those with the implant. Additionally, no evidence has been found that contraception influences body height (Warholm, Petersen, & Ravn, 2012). However, it is possible that contraception has an indirect effect on body mass by reducing competition for mates, which in turn, may reduce the driving pressure for males to be bigger.

In male chimpanzees, castration at a young age is likely to have a significant effect on body size and skeletal development (Kessler et al., 2016). The consequential reduction in testosterone causes a decline in bone and muscle mass, which in turn affects body mass (Kessler et al., 2016). There is also a delay or failure of the epiphyses to close which can result in increased stature (Clark & Gavan, 1962; Kessler et al., 2016). Consequently, captive individuals that are castrated early in life are likely to be smaller and lighter than their wild, non-castrated counterparts. Conversely, castration during adulthood is unlikely to affect stature but may result in a modest decline in body weight, as has previously been reported in rhesus monkeys (Michael & Wilson, 1974). However, as castration is only recommended for testicular pathology, it is very rarely used as a method of contraception in chimpanzees (AZA Ape TAG, 2010).

#### ***1.4 African Chimpanzee Sanctuaries***

Pan African Sanctuary Alliance (PASA) member sanctuaries provide homes for wild-born chimpanzees displaced by the bushmeat or pet trades, which have subsequently been confiscated by wildlife authorities (Wobber & Hare, 2011). These sanctuaries rehabilitate and provide high-quality, life-long care for primates with the aim to reintroduce healthy individuals into the wild (Wobber & Hare, 2011). Chimpanzees are quarantined when they first arrive at PASA sanctuaries, enabling staff to examine the individual and estimate its age based on dental development (chimpanzees are typically aged 2 – 3 years at arrival; Wobber & Hare, 2011). Any pre-existing injuries or health concerns are treated before the chimpanzee is placed into a temporary peer group of recent arrivals (Wobber & Hare, 2011). Once the chimpanzee is strong enough, it is permanently integrated into a mixed-age and mixed-sex social group, containing between 10 – 30 chimpanzees (Wobber & Hare, 2011). PASA sanctuaries offer forested enclosures with dozens of edible plant species for foraging, climbing and nesting, enabling chimpanzees to express species-typical behavior (Wobber & Hare,



2011). These enclosures range in size between 5 – 40 hectares, which can be between 10 – 100 times the size of the largest existing zoo enclosures (Wobber & Hare, 2011). On account of enclosure and group size, chimpanzees can create a fission-fusion social system approaching that of wild populations (Ongman, Colin, Raballand, & Humle, 2013; Wobber & Hare, 2011). PASA sanctuaries also supplement chimpanzees with local fruit and vegetables, which contain less sugars than domesticated fruits fed in zoological institutions (AZA Ape TAG, 2010). Collectively, sanctuaries significantly differ from research facilities and zoological institutions in the size of the simple enclosures, the quality of the environment and the diet that is provided to them. Accordingly, it has been proposed by Wobber and Hare (2011) that in comparison to other captive animals, PASA member sanctuaries offer an environment that enables the animals to live a life that is far more comparable to that of wild animals.

### ***1.5 Summary and Aims***

It is crucial to have a comprehensive understanding of growth and somatic maturation in chimpanzees from both a health and an evolutionary perspective. While previous literature has ascertained the normative growth pattern of body mass and crown-rump length in research facility populations (Gavan, 1953; Grether & Yerkes, 1940; Hamada & Udono, 2002; Hamada et al., 1996), our understanding of growth in wild chimpanzees is limited. Owing to methodological challenges associated with wild data, such as small sample sizes (Pusey et al., 2005), there are significant gaps in our current understanding of body mass development in wild chimpanzees. Further, no study to date has examined crown-rump length in this population. Nonetheless, previous literature has suggested discrepancies in the tempo of growth and body size between captive and wild chimpanzees (Kimura & Hamada, 1996; Zihlman et al., 2007), although no empirical data exist. Some have proposed that the calorie dense diet of captive populations, combined with their lower energy expenditure, results in comparatively more energy available for growth than wild populations (Hamada & Udono, 2006; Zihlman et al., 2007). Accordingly, growth parameters obtained from captive populations are unlikely to be appropriate for wild chimpanzees (Grether & Yerkes, 1940; Matsuzawa et al., 1990). African sanctuaries differ from research facility

and zoological institutions as they provide chimpanzees with vast expanses of primary forest in which they can forage for native plant species. Considering the similarities between the habitats and living conditions of wild and African sanctuary-based chimpanzees, it is possible that the growth of sanctuary animals may be more reflective of the growth of wild populations than zoological or research housed chimpanzees. However, to date the growth patterns of African sanctuary-based chimpanzees have not been assessed. Therefore, the aims of this study were two-fold; i) to characterise the growth rate and age at maturation for body mass and crown-rump length in male and female sanctuary chimpanzees, and ii) to compare the body mass of sanctuary chimpanzees to that of zoological populations and those housed in primate research facilities. It was hypothesised that in comparison to zoological and research facility counterparts, sanctuary chimpanzees would be lighter, have a slower rate of growth and have an older estimated age of body mass maturation.

## **2. Methods**

### **2.1 Population of sanctuary chimpanzees**

Routine health checks were conducted on 298 sanctuary chimpanzees (*Pan troglodytes*), aged 1 – 38 years. Single measurements of body mass were obtained from 150 males aged (mean  $\pm$  standard deviation; SD)  $14 \pm 8$  years and 148 females aged  $15 \pm 7$  years. Of these individuals, single measures of crown-rump length were available in 137 males and 140 females. Health checks were conducted between October 2013 and December 2018 at three African chimpanzee rehabilitation sanctuaries (Tchimpounga Chimpanzee Rehabilitation Centre, Congo; Chimfunshi Wildlife Orphanage, Zambia; Tacugama Chimpanzee Sanctuary, Sierra Leone). The three sanctuaries are members of PASA and the chimpanzees were cared for in accordance with the recommendations of the PASA operations manual (Farmer et al., 2009). Many of the chimpanzees were wild-born orphans confiscated by wildlife authorities. For these individuals, age was estimated based on dental development and records obtained by the sanctuary. For those animals born in the sanctuaries, their precise age was used. Animals were housed in semi-free ranging enclosures in mixed-sex and mixed-age groups that typically contain more than 15 individuals. Tchimpounga has three islands containing enclosures of 40 hectares (three of which are currently in use); Chimfunshi has six enclosures ranging from 19 –

77 hectares and Tacugama has five enclosures that are approximately 2.5 hectares. Chimpanzees have access to range vegetation during the day and the option of indoor dormitories at night. Supplementary fruit, vegetables and grains were obtained locally and provided to chimpanzees at routine points throughout the day. All procedures and protocols involved in this study were endorsed by the PASA Advisory Council and Cardiff Metropolitan University, UK and approved by the British and Irish Association of Zoos and Aquariums.

## **2.2 Anaesthesia**

Prior to each health check, animals were anaesthetised using one of the following protocols: i) combination of medetomidine (0.03 - 0.05 mg/kg) and ketamine (3 - 5 mg/kg) delivered intramuscularly via hand injection or remote dart injection ( $n = 172$ ); ii) combination of tiletamine-zolazepam (2 mg/kg) and medetomidine (0.03 mg/kg) via remote dart injection ( $n = 68$ ); iii) tiletamine-zolazepam (10 mg/kg) via remote dart injection ( $n = 31$ ); iv) combination of tiletamine-zolazepam (2 mg/kg) and ketamine (5 mg/kg) ( $n = 27$ ). The anaesthetic protocol used was determined by the lead veterinarian at each chimpanzee rehabilitation sanctuary and the dosage was based on either an estimated body mass or data from previous health checks. Animals were monitored throughout the procedure until recovery.

## **2.3 Measurements of sanctuary chimpanzees**

Body mass and crown-rump length were measured during each health check. Body mass was collected using either a calibrated hanging scale (Salter Brecknell, 235-6S, West Midlands, UK) or Seca electronic weighing scales (Seca, Vogel and Halke, Hamburg, Germany), and was assessed to the nearest 0.1 kg. Crown-rump length was measured with the animal positioned in lateral recumbency, taken from the pole of the head to the base of the rump at the coccyx (Fig.1). All measurements were taken with a measuring tape and were assessed to the nearest 0.5 cm, by one researcher.



**Figure 1.** Illustration of crown-rump length measurement in a chimpanzee (*Pan troglodytes*). The length from the pole of the head to the base of the rump at the coccyx was measured whilst the animal was in lateral recumbency.

## **2.4 Data analysis**

### **2.4.1 Zoological population**

Unidentified body mass measurements from zoological chimpanzees were acquired from the Species360 Zoological Information Management System (2019), a comprehensive database that curates information recorded by a global network of zoological collections. Measurements included in this analysis were obtained during health assessments at zoological collections across Europe and the United States of America, conducted between 1980 and 2019. A total of 454 males aged (mean  $\pm$  SD)  $19 \pm 11$  years, and 623 females aged  $21 \pm 11$  years, were included in the final analysis. These data were initially screened for obvious data input errors, then outliers were identified using the robust regression and outlier removal (ROUT) method (Q set to 1%) in GraphPad Prism (GraphPad Prism for Windows, version 8.0.1, San Diego, CA) and were removed from the analysis ( $n = 50$  males and  $n = 102$  females). To prevent any confounding effect of repeated measures on the analysis, a single body mass measurement was randomly selected from each chimpanzee included in the database

using the RAND function in Microsoft Excel (2016). Additionally, to ensure the dataset was age-comparable to the sanctuary chimpanzees, only animals between the ages of 1 - 40 years were included.

#### *2.4.2 Characterisation of growth in sanctuary and zoological populations*

Sex-specific piecewise linear least squares regressions were used to model crown-rump length in sanctuary chimpanzees and body mass in sanctuary and zoological populations. This method uses a best-fit (unconstrained) analysis to identify a pair of linear lines and the breakpoint between these two lines (Altmann & Alberts, 2005). The slope of the regression line to the left of the breakpoint can be used as an estimate of growth rate (Altmann & Alberts, 2005; Huck et al., 2011) and the breakpoint as the estimated age at which maturation of crown-rump length/body mass occurs (Leigh, 1994a; Leigh & Terranova, 1998). The slope of the regression line to the right of the breakpoint can be interpreted as the relatively stable period following maturation, where asymptotic (adult) crown-rump length/body mass has been reached (Leigh, 1994a; Leigh & Terranova, 1998). It is important to note that as this analysis only involves cross-sectional data, the growth parameters indicated by the regression analysis are estimations. The slopes of the lines and the breakpoints were compared statistically to assess within sex differences and same-sex group differences, between sanctuary and zoological populations. The size of the effect was calculated to estimate the magnitude of the within sex and same-sex group differences using Cohen's  $f^2$  (1988); here  $f^2 = R^2_{\text{adj}} / (1 - R^2_{\text{adj}})$ , where  $R^2$  = the coefficient of determination from the pooled (shared) regression model for the two groups involved in the comparison. By convention, it can be interpreted in terms of small ( $f^2 \leq 0.02$ ), medium ( $f^2 \leq 0.15$ ) or large ( $f^2 \geq 0.35$ ) effects (Cohen, 1988). Regression analyses were performed using GraphPad Prism.

Average adult body mass and crown-rump length was calculated for each sex and each population by averaging all measurements occurring after the identified breakpoint. Distribution of the residuals were first assessed for normality. Age was considered to be normally distributed for both sexes of the sanctuary and zoological populations as the skewness and kurtosis values were within  $\pm 1.96$  (Kim, 2013). Crown-rump length of the sanctuary population was normally distributed according to the Shapiro-Wilk test and was subsequently compared between sexes using an

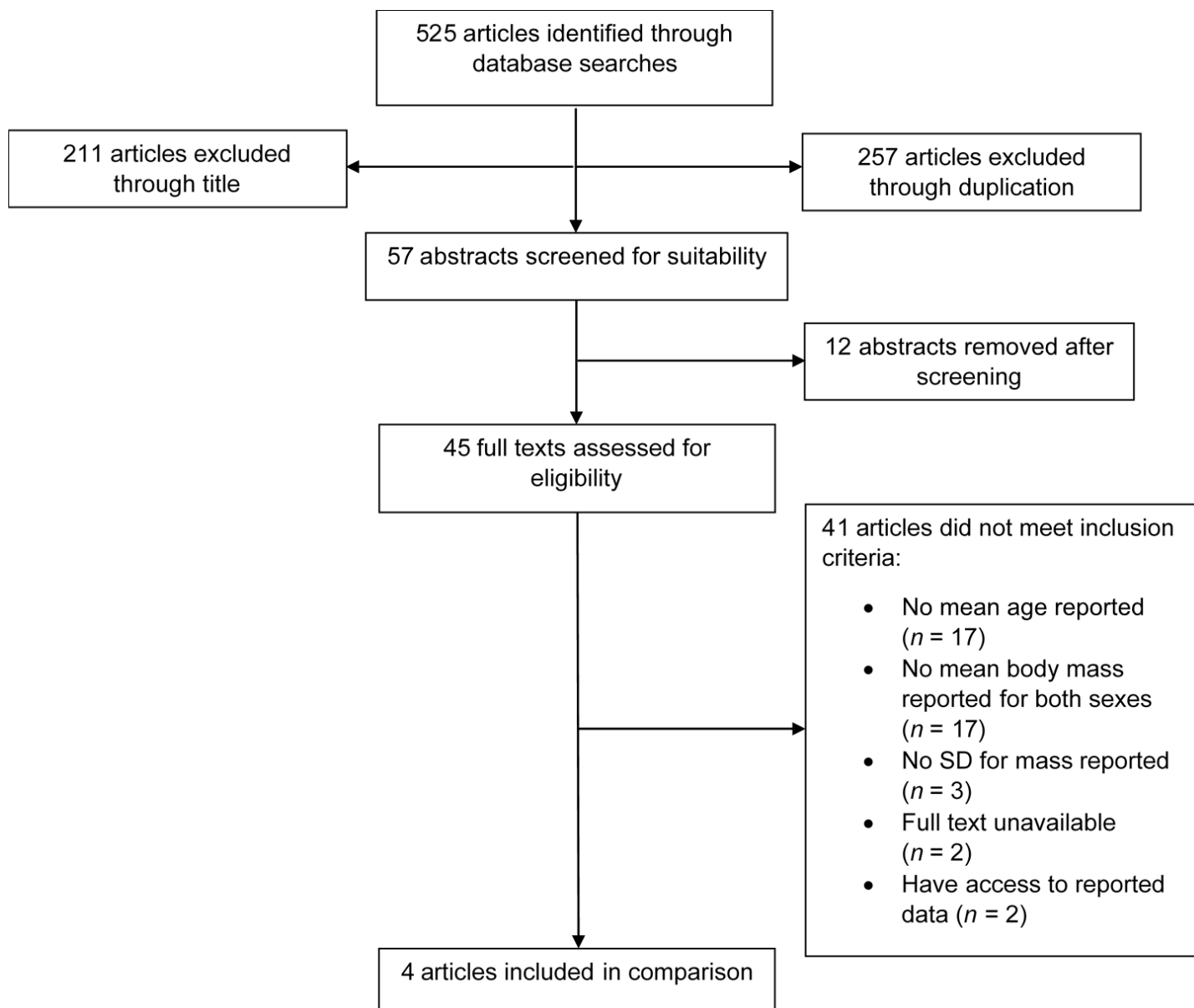
independent samples student's t-test and presented as the mean  $\pm$  SD. The effect size for crown-rump length was calculated as Cohen's  $d$ ; here,  $d = ((M_1 - M_2)/[SD_1 + SD_2]/2]$ , where  $M_1$  = mean of group 1 and  $M_2$  = mean of group 2,  $SD_1$  = standard deviation of group 1, and  $SD_2$  = standard deviation of group 2. An effect size of  $\leq 0.2$  can be deemed a small effect,  $\leq 0.5$  a medium effect, and  $\geq 0.8$  a large effect size (Cohen, 1988). Body mass of sanctuary and zoological populations were not normally distributed according to Shapiro-Wilk tests, and therefore Man-Whitney U tests were performed to assess sex differences within, and same-sex differences between populations. Effect sizes for body mass were estimated using Glass rank biserial correlation coefficient ( $r_G$ );  $r_G = 1 - (2U/(n_1 \times n_2))$ , where  $U$  = Mann Whitney U statistic,  $n_1$  = sample size of group 1 and  $n_2$  = sample size of group 2. For effect size calculations,  $r_G \leq 0.1$  can be interpreted as a small effect;  $r_G \leq 0.3$  a medium effect and  $r_G \geq 0.5$  a large effect (Kerby, 2014). Adult body mass data are presented as the median (interquartile range; IQR) for each sex. Sex differences were analyzed using IBM SPSS statistical software version 25 (SPSS, Chicago, Illinois, USA). For all statistical analyses, alpha was set at  $P < 0.05$ . The potential of sexual dimorphism in crown-rump length and body mass were assessed by calculating the sex ratio (male variable/female variable) in adults (i.e. all individuals to the right of the identified breakpoint).

#### 2.4.3 Body mass of primate research facility populations

Previously published data on the body mass of chimpanzees housed in primate research facilities were identified through a literature search of peer-reviewed publications published before March 2019. Unfortunately, too few data were available to also examine crown-rump length (only two articles were identified in the search). The literature search was conducted via electronic searches of three databases; PubMed, Scopus and PrimateLit and the following key terms were used to search for relevant articles: *body mass*, *body weight*, *chimpanzee*, *Pan troglodytes* and *obese*. The inclusion criteria for eligible studies was i) to be written in the English-language; ii) to include a mean age  $\pm$  SD for both male and female chimpanzee populations; iii) to include mean body mass  $\pm$  SD for both male and female chimpanzee populations. Any article that presented body mass from the Alamogordo Primate Facility colony (Holloman Airforce Base, Alamogordo, New Mexico) or from any of the three

chimpanzee rehabilitation sanctuaries involved were not included as the author had access to the raw data from these populations ( $n = 2$ ). The search process is illustrated in Figure 2. A total of four articles were included in the final analysis; Andrade et al. (2011), Bribiescas and Anestis (2010), Grether and Yerkes (1940) and Smith et al. (1975), which are summarised in Table 1. For all included articles, 95% confidence intervals (CI) were calculated for the mean age and mean body mass. In addition to the four primate research facilities identified in the literature, the author had access to body mass data from 76 male (aged  $29.7 \pm 8.5$  years) and 55 female (aged  $28.6 \pm 9.5$  years) National Institute of Health-owned chimpanzees, from the Alamogordo Primate Facility colony. The mean age (95% CI) and mean body mass (95% CI) were calculated for each sex and were included in the final comparison of body mass between chimpanzees housed in sanctuaries, zoological collections and primate research facilities. The data from each of the primate research facilities were subsequently plotted alongside the piecewise linear regressions of sanctuary and zoological chimpanzees. Additionally, average adult body mass was calculated for each sex of the Alamogordo Primate Facility colony and was subsequently compared to that of the sanctuary population using a Man-Whitney U test.

No comparison could be made to wild populations as the literature search did not identify any articles that met the inclusion criteria. In most cases, articles containing wild data either did not report an average age or the average body mass was reported as the median (IQR).



**Figure 2.** Flow diagram illustrating the process used in the selection of articles containing body mass data of chimpanzees (*Pan troglodytes*) housed in primate research facilities.



**Table 1.** Summary of the four research facility populations included in the comparison of chimpanzee (*Pan troglodytes*) body mass between different living environments. Ages are presented as mean  $\pm$  SD.

Reference	Males		Females		Housing	Diet
	<i>n</i>	Age (years)	<i>n</i>	Age (years)		
<b>Smith et al., 1975</b>	25	13.3 $\pm$ 1.4	20	14.3 $\pm$ 2	-	-
<b>Bribiescas and Anestis, 2010</b>	26	2.8 $\pm$ 1.8	11	2.8 $\pm$ 1.9	Socially housed. Climate-controlled indoor (5 x 3 x 3 m) and outdoor area (5 x 6 x 5 m).	Teklad NIB primate diet, fresh fruit/produce once daily.
	10	8.3 $\pm$ 1.3	16	10.8 $\pm$ 1.8		
	11	33.5 $\pm$ 6.3	22	23.4 $\pm$ 7.4		
<b>Andrade et al., 2011</b>	17	21.8 $\pm$ 7.2	22	23.8 $\pm$ 10.9	Groups of 2 - 5 chimpanzees in stainless steel cages with indoor-outdoor access.	Monkey Diet, seasonal fresh fruit and vegetables twice daily.
<b>Grether and Yerkes, 1940</b>	19	0 - 17†	33	0 - 17†	-	-

†Age range.

### 3. Results

#### 3.1 Characterisation of growth in sanctuary chimpanzees

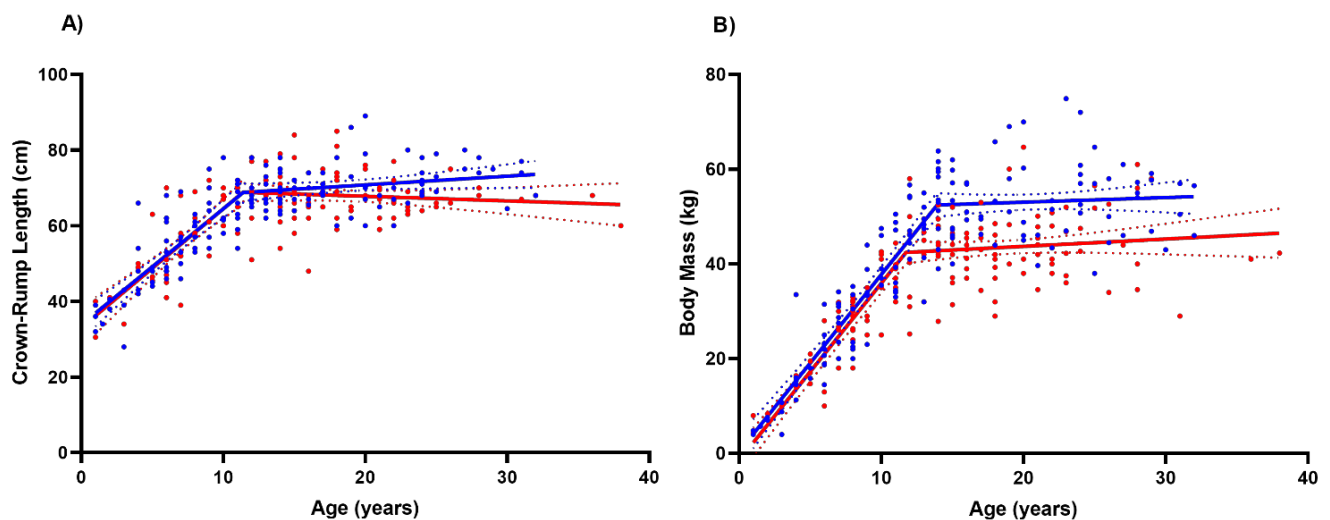
##### 3.1.1 Crown-rump length

The overall range of crown-rump lengths from the sanctuary population is shown in Table 2 and the piecewise regressions are illustrated in Figure 3A ( $R^2 = 0.72$  for males;  $R^2 = 0.56$  for females; Cohen's  $f^2 = 0.64$ ). Regression analysis indicated the breakpoint for crown-rump length was similar between sexes, occurring at 11.4 years in both males and females ( $F_{1, 268} = 0.00004$ ,  $P = 0.983$ ). Additionally, no difference was identified in the estimated growth rate of males and females (males: 3.06 cm/year vs. females: 3.14 cm/year;  $F_{1, 268} = 0.03$ ,  $P = 0.866$ ), but there was a difference between

the regression slopes after the breakpoint; males: 0.23 cm/year vs. females: -0.12 cm/year ( $F_{1, 268} = 193.1$ ,  $P = < 0.001$ ). The adult crown-rump length was greater in males than females (mean  $\pm$  SD;  $71 \pm 6$  cm vs.  $68 \pm 7$  cm;  $t(161) = -2.6$ ,  $P = 0.011$ ;  $d = 0.38$ ) and the sex-ratio for crown-rump length was 1.04.

**Table 2.** Range of crown-rump length and body mass values for male and female sanctuary and zoological chimpanzees (*Pan troglodytes*).

	Age (years)	Crown-rump length (cm)	Body mass (kg)
<b>Sanctuary males</b>	1 - 32	28 - 89	4.0 - 74.9
<b>Sanctuary females</b>	1 - 38	31 - 86	4.3 - 64.7
<b>Zoological males</b>	1 - 40	-	3.0 - 108.4
<b>Zoological females</b>	1 - 40	-	3.3 - 99.0



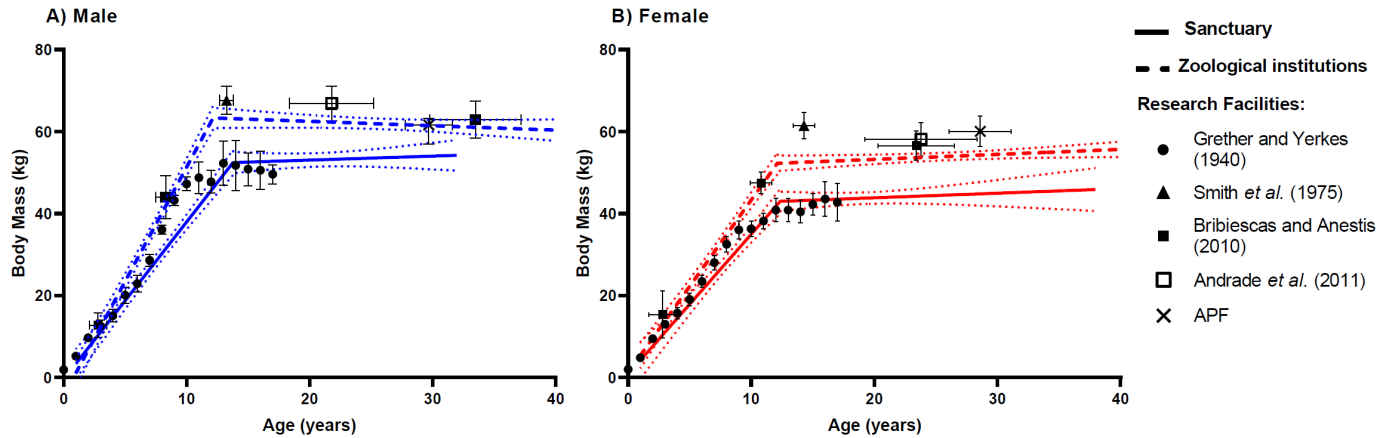
**Figure 3.** Observed growth of crown-rump length (A) and body mass (B) in male (blue) and female (red) African sanctuary chimpanzees (*Pan troglodytes*), fitted with unconstrained piecewise linear least squares regressions. 95% CI are shown, represented by dotted lines.

### 3.1.2 Body mass

The overall range in body mass for sanctuary animals is summarised in Table 2 and the piecewise regressions are shown in Figure 3B ( $R^2 = 0.82$  for males;  $R^2 = 0.69$  for females; Cohen's  $f^2 = 3.41$ ). The breakpoint in female chimpanzees was estimated at 12.4 years of age, approximately one year before males (12.4 years vs. 13.8 years;  $F_{1, 289} = 2.7$ ,  $P = 0.103$ ). However, the estimated rates of body mass growth prior to the breakpoint (males: 3.84 kg/year vs females: 3.39 kg/year;  $F_{1, 289} = 1.1$ ,  $P = 0.303$ ) and the slopes of the regression lines after (males: 0.1 kg/year vs. females: 0.11 kg/year;  $F_{1, 289} = 0.01$ ,  $P = 0.943$ ) were similar between sexes. Adult body mass was greater in males compared to females (median [IQR]; males: 52 [11.15] kg vs. females: 43.4 [7.5] kg;  $U = 1, 704.5$ ,  $P = < 0.001$ ;  $r_G = 0.58$ ), and the sex-ratio for body mass was 1.21.

### 3.2 Body mass comparison between sanctuary and zoological chimpanzees

As with the sanctuary comparisons, the age and body mass range for chimpanzees in zoological collections is summarised in Table 2, and the piecewise regressions for body mass are shown in Figure 4 ( $R^2 = 0.72$  for males;  $R^2 = 0.62$  for females; Cohen's  $f^2 = 2.01$ ). Zoological males had a greater estimated growth rate in comparison to females (males: 5.58 kg/year vs. females: 4.21 kg/year;  $F_{1, 1069} = 8.5$ ,  $P = 0.004$ ), but no sex difference was observed in the estimated breakpoints (males: 12.2 years vs. females: 12.1 years;  $F_{1, 1069} = 0.002$ ,  $P = 0.968$ ). The slope of the regression line following the breakpoint was significantly greater in zoological females compared to males (males: -0.11 kg/year vs. females: 0.12 kg/year;  $F_{1, 1069} = 397.7$ ,  $P = < 0.001$ ). Additionally, median adult body mass was significantly heavier in zoological males compared to females (median [IQR]; males: 60.9 [15.0] kg vs. females: 52.3 [12.8] kg;  $U = 96, 610$ ,  $P = < 0.001$ ;  $r_G = 0.43$ ), and the sex ratio for body mass equaled 1.15.



**Figure 4.** Comparison of body mass between male (A) and female (B) sanctuary, zoological and research facility populations of chimpanzee (*Pan troglodytes*). Body mass of sanctuary chimpanzees (represented by solid line) and those housed in zoological facilities (represented by dashed line) were fitted with a piecewise linear least squares regression, with 95% CI shown (represented by dotted lines). Symbols represent mean body mass of research facility chimpanzees with 95% CI shown for mass and age (represented by error bars). Symbols represent previously published data; filled square represents Bribiescas and Anestis (2010); filled circle represents Grether and Yerkes (1940); triangle represents Smith et al. (1975); unfilled square represents Andrade et al. (2011); cross represents Alamogordo Primate Facility (APF) colony.

In comparison to their sanctuary counterparts, both zoological males and females were estimated to attain maturation at a younger age (male breakpoints; zoological: 12.2 years vs. sanctuary: 13.8 years,  $F_{1, 596} = 2.3$ ,  $P = 0.128$ ; female breakpoints; zoological: 12.1 years vs. sanctuary: 12.4 years,  $F_{1, 762} = 537.2$ ,  $P = < 0.001$ ). Additionally, male chimpanzees from zoological collections had a greater estimated growth rate compared to those from sanctuaries (zoological: 5.58 kg/year vs. sanctuary: 3.84 kg/year,  $F_{1, 596} = 781.7$ ,  $P = < 0.001$ ). In contrast, no significant difference was observed between the estimated growth rates of zoological and sanctuary females, despite a marginally steeper slope in the former (zoological: 4.21 kg/year vs. sanctuary: 3.39 kg/year,  $F_{1, 762} = 2.03$ ,  $P = 0.155$ ). The slopes of the regression lines following the breakpoint were also not different between sanctuary

and zoological populations, for either sex (zoological males: -0.11 kg/year vs. sanctuary males: 0.1 kg/year,  $F_{1, 596} = 0.7$ ,  $P = 0.412$ ; zoological females: 0.12 kg/year vs. sanctuary females: 0.11 kg/year,  $F_{1, 762} = 0.002$ ,  $P = 0.968$ ). A large effect size was found for the same-sex group regression comparisons; for males, Cohen's  $f^2 = 2.90$  and for females, Cohen's  $f^2 = 0.67$ . Additionally, both adult males (median [IQR]; zoological: 60.9 [15.0] kg vs. sanctuary: 52 [11.5] kg;  $U = 19, 247$ ,  $P = < 0.001$ ,  $r_G = 0.5$ ) and females (median [IQR]; zoological: 52.3 [12.8] kg vs. sanctuary: 43.4 [7.5] kg;  $U = 8, 506.5$ ,  $P = < 0.001$ ;  $r_G = 0.58$ ) housed in zoological collections were significantly heavier than those in sanctuaries.

### ***3.3 Body mass comparison between sanctuary and primate research facility chimpanzees***

A visual comparison of body mass between sanctuary chimpanzees, zoological chimpanzees and primate research facilities is shown in Figure 4. In comparison to the research facilities identified in the literature search, sanctuary animals typically weighed less, although the Yale Laboratories population (Grether & Yerkes, 1940; represented by filled circles in Figure 3) was a notable exception. The difference in body mass was particularly exaggerated in females, where excluding Grether and Yerkes (1940), no overlap was seen in the CI of body mass between sanctuary and primate research facility chimpanzees. Furthermore, adult males (median [IQR]; APF: 61 [11.8] kg vs. sanctuary: 52 [11.5] kg;  $U = 1, 127.5$ ,  $P = < 0.001$ ) and females (median [IQR]; APF: 58 [16.5] kg vs. sanctuary: 43.4 [7.5] kg;  $U = 489$ ,  $P = < 0.001$ ) from the Alamogordo Primate Facility (APF) colony (for which the author had access to the raw data) were significantly heavier than those in sanctuaries.

## **4. Discussion**

We provide the first data on the growth patterns of body mass and crown-rump length in sanctuary chimpanzees, a population of semi-free ranging animals which inhabit an environment that, in comparison to either zoological collections or primate research facilities, more closely resembles that of wild chimpanzees (Wobber & Hare, 2011). The main outcomes from this study are four-fold; i) sanctuary chimpanzees exhibit

minimal sexual dimorphism in crown-rump length and the rate of body mass growth; ii) maturation of body mass occurred approximately one year earlier in female sanctuary chimpanzees compared to their male counterparts; iii) estimated growth rates were greater and age at maturation was younger in zoological chimpanzees compared to animals in sanctuaries; and iv) animals housed in zoological facilities were heavier compared to those in sanctuaries. These data highlight the influence of environment on body mass, suggesting that this needs to be considered carefully when utilising zoological or research housed chimpanzees to investigate life history characteristics of the species.

#### ***4.1 Crown-rump length***

No distinct sex differences were observed in the growth patterns of crown-rump length in sanctuary chimpanzees. However, following the breakpoint, the slope of the regression line increased slightly in males and reduced slightly in females. Owing to the cross-sectional nature of the data, this may be reflective of individual variation in crown-rump length. Alternatively, the negative slope in females could reflect a modest decline in crown-rump length with increasing age. This decline is unlikely to be related to nutrition as older adult females are of a similar mass to those of a younger age. One possibility is a loss of bone density in geriatric females, which has been documented in wild chimpanzees (Carlson et al., 2008; Gunji et al., 2003; Sumner, Morbeck, & Lobick, 1989). It is possible that age-related bone loss may result in a shrinkage of the vertebrae or vertebral discs, similar to the osteoporotic process observed in humans, causing individuals to become slightly smaller with advancing age (Sanila, Kotaniemi, Viikari, & Isomaki, 1994). A decline in bone density has been associated with diminished oestrogen levels in postmenopausal humans and the same association may be present in geriatric female chimpanzees. However, the existence of the menopause in chimpanzees is contentious as fertility can continue until the sixth decade of life, approximately their maximum lifespan (Herndon et al., 2012).

There are only a handful of previous studies that have reported sex-specific crown-rump lengths of adult chimpanzees. Videan et al. (2007) reported average crown-rump lengths of 68 cm for both male and female chimpanzees from the Primate Foundation of Arizona. However, Hamada and Usono (2006) reported maximum crown-rump

lengths of 84.5 cm for males and 81 cm for females in a research facility, which are considerably greater than the sanctuary chimpanzees in this study. Differences in nutrition and physical activity may partly explain the size variation observed between the chimpanzees in the sanctuaries and those reported by Hamada and Usono (2006). Sanctuary chimpanzees are likely to have a diet of greater variety and lower calorific content than research facility animals, which could contribute to their smaller size. Additionally, it is possible that air pollution may also be a contributing factor, which has been associated with a reduced height for age in humans (Huang, Leung, & Schooling, 2018). Furthermore, phylogenetic variation between subspecies could also be responsible, as Morbeck and Zihlman (1989) have previously identified *Pan troglodytes schweinfurthii* have smaller dimensions compared with other *Pan troglodytes*. However, in the present study, the subspecies of the sanctuary animals is unknown and Hamada and Usono (2006) did not report such information, hence a comparison is not possible. Hamada and Usono (2006) also reported the maximum crown-rump lengths were attained at 13.8 years in males and 15.7 years in females. This would suggest that the research facility chimpanzees studied by Hamada and Usono had a far longer period of growth than the sanctuary chimpanzees in this study. While this was unexpected, Hamada and Usono (2006) reported limited detail of their methodology, and so it is unclear how age of maturation was estimated.

## **4.2 Body mass**

### **4.2.1 The growth pattern of sanctuary chimpanzees**

Prior to maturation, male chimpanzees were estimated to gain body mass over a longer period and at a marginally greater rate, compared to their female counterparts. This can likely be attributed to elevated levels of testosterone in males, which promotes skeletal muscle hypertrophy and the development of comparatively heavier bones (Kemnitz et al., 1988). Previously, Kemnitz et al. (1988) demonstrated that androgens, the group of steroid hormones to which testosterone belongs, were responsible for stimulating the sex difference in body mass of rhesus macaques (*Macaca mulatta*). Although no similar research has been conducted in chimpanzees, testosterone has been reported to rapidly increase in male chimpanzees in research facilities at approximately seven years of age (Behringer, Deschner, Deimel, Stevens, & Hohmann, 2014; Copeland, Eichberg, Parker, & Bartke, 1985; Martin, Swenson, &

Collins, 1977). It is possible that an increase in testosterone in juvenile males explains the marginally greater growth rate observed in sanctuary males. Female chimpanzees, in contrast, exhibit much lower levels of testosterone, corresponding with their lower growth rates (Copeland et al., 1985).

The observed sexual dimorphism in the body mass of sanctuary chimpanzees appears to primarily result from sex differences in the duration of the growth period. While this finding is consistent with Hamada et al. (1996), it is in contrast to that proposed by Leigh and Shea (1995), who suggested that sex differences in the rate of growth primarily account for sexual dimorphism in *Pan troglodytes*. The pace of growth reflects an individual's physiological energy expenditure, whereby greater resources result in a greater growth rate (Pontzer et al., 2014). As there are significant differences between the environment of sanctuaries and research facilities, such as enclosure size, diet and feeding competition (which are more comprehensively discussed in section 4.2.2), it is likely that research chimpanzees have comparatively more energy to devote to growth, and hence have a greater growth rate and shorter duration of growth.

#### *4.2.2 The effect of living environment on body mass*

In agreement with the experimental hypotheses, the sanctuary chimpanzees were lighter than those living in zoological and primate research facilities. Additionally, the sanctuary chimpanzees were estimated to have a slower rate of growth and attain maturation at an older age, compared to their zoological counterparts. These differences may be explained by energy expenditure and nutrition, which likely varies considerably between rearing environments. Zoological and research facility populations are likely to have comparatively more energy available for growth than sanctuary chimpanzees as they are housed in smaller enclosures, in which they are not required to search or compete for food (Zihlman et al., 2007). Moreover, zoological and research facility chimpanzees have a diet of greater calorific content than sanctuary populations, as a staple portion of their diet consists of commercial monkey biscuit (AZA Ape TAG, 2010). Zoological chimpanzees are also fed domesticated fruit containing more simple sugars than those obtained in natural habitats and are frequently provided with food for enrichment during the day (AZA Ape TAG, 2010). Whereas in sanctuaries, animals inhabit much larger enclosures which can be 10 –



100 times the size of the largest existing enclosure at a zoological institution (Wobber & Hare, 2011). Furthermore, the enclosures within African sanctuaries contain diverse natural vegetation (Wobber & Hare, 2011) and the animals are supplemented with local fruits and vegetables.

The body mass of chimpanzees is also likely influenced by the size of the animals' social group. In the wild, chimpanzee communities can contain up to 120 members (Nishida, 1968). Although three of the articles examining animals from research facilities did not report the number of chimpanzees housed in each group (Bribiescas & Anestis, 2010; Grether & Yerkes, 1940; Smith et al., 1975), Andrade et al. (2011) noted that chimpanzees lived in small groups of 2 – 5 animals. Chimpanzees in zoological institutions are typically housed in groups of more than five individuals (AZA Ape TAG, 2010), but these groupings are often far smaller than those in the African sanctuaries included in this study, which more closely resemble those of wild populations. Housing chimpanzees in small groups can have a detrimental effect on body mass as it prevents the animal from engaging in a complex social hierarchy, which may reduce competition for food. This is of particular concern for female chimpanzees, who will compete for food as their reproductive success is dependent on it (Pusey & Schroepfer-Walker, 2013). In zoological and primate research facilities, competition for food is largely removed, allowing females to consume as much as they are provided. This likely enables female body mass to increase to such an extent where no, or reduced, sexual dimorphism is observed, as is seen in the zoological chimpanzees and three of the research facility populations used in the present study (Andrade et al., 2011; Smith et al., 1975; APF). Increased weight gain could be detrimental to the wellbeing of female chimpanzees, as it has been associated with a rise in systolic blood pressure (Ely et al., 2013), and may be associated with the apparent prevalence of cardiac disease in zoological and research chimpanzees (Lammey, Lee, Ely, & Sleeper, 2008; Strong et al., 2020). However, it is important to note that the body mass measurements of zoological chimpanzees used in this analysis were collected between 1980 to 2019. Over this time period, there have been considerable improvements in the husbandry of zoos, particularly to diet (Kirkwood, 2003), which may have affected the growth of the animals. Consequently, it is possible that the body mass observed for the zoological chimpanzees is not wholly reflective of the present time. Unfortunately, it was not possible to assess the effect of time in this

analysis as, for anonymity, Species360 could not disclose the year in which each health check was conducted.

A notable exception to the rest of the primate research facilities included in this comparison were the animals from the Yale Laboratories population (Grether & Yerkes, 1940), which appeared to closely track the growth patterns of the sanctuary chimpanzees. This could possibly be explained by changes in animal husbandry procedures in the years that followed the Grether and Yerkes (1940) publication, as many of the other data were published after 2000 (Andrade et al. 2011; Bribiescas & Anestis, 2010; Alamogordo Primate Facility). However, as Grether and Yerkes (1940) did not provide details on the husbandry of the chimpanzees, it is difficult to fully discern the reason for this disparity.

It has been proposed that the stress experienced by orphan chimpanzees early in life may also influence body growth (Walker, Walker, Goodall, & Pusey, 2018). In wild chimpanzees, Walker et al. (2018) identified that sexual maturity was delayed in individuals that were orphaned prior to 8 years of age, which could have influenced the timing of body maturation. Further, wild orphans also had significantly less muscle than their non-orphaned age-matched counterparts (Samuni et al., 2020). Samuni et al. (2020) proposed that the psychological stress experienced by orphan chimpanzees, combined with reduced access to food resources, may result in suppression of growth and muscle development. However, as there is limited evidence of lasting behavioral and psychological damage in orphan sanctuary chimpanzees (Wobber & Hare, 2011), stress is unlikely to affect growth in this population. Furthermore, despite the nutrient-poor environment that an orphan has come from, PASA sanctuaries provide rich physical and social environments, with plentiful resources (Wobber & Hare, 2011). This favourable change in environment can promote 'catch-up growth', whereby the growth rate of an individual is accelerated, enabling its genetically determined target size to be attained (Hamada & Udono, 2002). Consequently, it is unlikely that early life stress will have any long-lasting effect on orphan body size in the PASA sanctuaries assessed.

#### *4.2.3 Age at maturation*

The age of chimpanzee body mass maturation appears to vary between sanctuary, zoological and primate research facilities. In this study, maturation of body mass was

estimated to occur at an older age in sanctuary chimpanzees compared to their zoological counterparts. No definitive age has been suggested for maturation in research facility chimpanzees, but previous literature typically suggests a range of 12 - 15 years of age, depending on sex. Research facility females are commonly reported to cease growth before their male counterparts, with estimates of 11.5 - 12.5 years of age for females (Hamada et al., 1996; Leigh & Shea, 1996) and 12 – 15 years of age for males (Hamada et al., 1996; Leigh & Shea, 1996; Smith et al., 1975). Overall, this would suggest that the sanctuary chimpanzees experience maturation at an older age than their zoological counterparts and some of the research facility populations. This earlier onset of maturation in zoological and research facility animals could be associated with a greater body mass, as has previously been documented in overweight and obese humans (Chung, 2017). Additionally, endocrine disrupting chemicals such as pesticides may influence the timing of maturation by accelerating puberty (Ozen & Darcan, 2011), but the level of pesticide residue in the diet of the chimpanzees (for all living environments) is unknown. Interestingly, the female research facility chimpanzees examined by Hamada and colleagues (1996) were of a comparable maturation age to the sanctuary chimpanzees from this study. In previous literature, the age at maturation of research facility populations have typically been visually estimated using LOESS smoothing curves (Hamada et al., 1996; Leigh & Shea, 1996), whereas an unconstrained piecewise linear regression was used in this analysis. This may, therefore, explain the similarity between the maturation ages of those reported by Hamada et al. (1996) and the sanctuary animals in this study.

#### *4.2.4 Body mass of wild populations*

Unfortunately, previously published data on the body mass of wild chimpanzees were not available for comparison in this study, as those published did not meet the inclusion criteria. Despite this, several publications have reported the average body mass for adult chimpanzees in the wild. Pusey et al. (2005) reported median body mass as 39.0 kg (SE 1.22) for 23 adult males and 31.3 kg (SE 0.87) for 15 adult females of Gombe National Park (*Pan troglodytes schweinfurthii*). Uehara and Nishida (1987) have reported slightly greater average values of 42.0 kg for six adult males and 35.2 kg for eight adult females of the Mahale Mountains (*Pan troglodytes schweinfurthii*), which is consistent with reports of the same subspecies in eastern Zaire (Rahm, 1967 in Uehara & Nishida, 1987). One article predicted an even greater body mass for *Pan*

*troglodytes schweinfurthii* in the Kibale Forest, based on skeletal remains (46.3 kg and 53.7 kg for two adult males and 40.5 kg for an adult female; Peterhans, Wrangham, Carter & Hauser, 1993). The age at maturation is also not commonly reported in wild chimpanzees due to the difficulties of assessing growth in this population. Pusey (1978) suggested 15 years of age for Gombe males, which is approximately a year after the estimated age in the sanctuary males. While no direct age-matched comparison can be made, these articles would suggest that sanctuary chimpanzees are likely heavier and their maturation occurs at a younger age than most documented populations in the wild. One likely explanation for this is the disparity in food availability between wild and sanctuary animals and the amount of stress associated with searching for it. Additionally, subspecies variation might also contribute to the difference in body mass. For the present analysis, data were collected from three chimpanzee rehabilitation sanctuaries located across Africa, all of which received orphans from varying locations. Accordingly, the sanctuary chimpanzees are likely to include a mix of subspecies which could, on average, be of greater mass than the wild populations reported (primarily *Pan troglodytes schweinfurthii*). However, it should be noted that any comparison to wild data is extremely problematic as the available data is scarce compared to captive populations and the sample sizes are much smaller.

#### **4.3 Limitations and Future Directions**

The unconstrained piecewise linear regression method adopted in this study was beneficial for identifying the estimated ages at maturation, but it does provide a simplistic view of growth rates by assuming they are constant. Alternative methods, such as pseudovelocity curves applied by Hamada and Udon (2002), can visually demonstrate how growth rates fluctuate with age, but cannot be used for statistical comparison. Additional longitudinal studies are required to comprehensively investigate fluctuations in the growth rates of sanctuary chimpanzees and how these compare to other captive populations. Secondly, the sanctuary population used in this analysis were highly likely to be heterogeneous in terms of subspecies and it is possible that some of the disparities seen between sanctuary, zoological and research facility populations could be partially explained by phylogenetic variation. Further work investigating the subspecies of the sanctuary chimpanzees would be beneficial to

clarify its impact on growth. Additionally, whilst the majority of the sanctuary chimpanzees included in this analysis arrived at the sanctuary as infants, a small number may have been older on arrival and hence, their growth would not reflect an upbringing in sanctuary conditions. The author also did not have access to data in wild chimpanzees, so the findings of this study are limited to captive populations. Future research should aim to assess how the growth of wild populations statistically compares to its captive counterparts. Furthermore, no attempt was made in this analysis to control for seasonal variation, which is known to influence body mass (Pusey et al., 2005). Body mass of the sanctuary chimpanzees were collected during routine health checks, the timing of which varied slightly between sanctuaries and was out of the author's control. Finally, body mass measurements of zoological chimpanzees were acquired from an electronic database that curates information recorded by a global network of zoological collections. It is therefore highly likely that body mass was measured by numerous assessors using different models of weighing scales, all of which could have introduced a potential source of error. While the same researcher measured all of the sanctuary chimpanzees, intra-observer reliability was not assessed owing to time-constraints during anesthesia. Further, the weighing scales used to assess body mass in the sanctuary population were not consistent between sanctuaries. No previous research exists for inter- and intra-observer reliability in body mass or crown-rump length measurements for chimpanzees, but previous research in human populations has identified a very high coefficient of variability ( $> 0.99$ ) in both children (Stomfai et al., 2011) and adults (Sebo, Beer-Borst, Haller, & Bovier, 2008).

#### **4.4 Conclusion**

This study contributes to current understanding of chimpanzee growth and highlights the marked influence of environment on the maturation characteristics of body mass and crown-rump length in chimpanzees. These data confirm that animals in natural environments, such as sanctuaries, demonstrate a comparatively reduced rate of growth, delayed maturation and smaller body mass than those in research facilities or zoological institutions. Consequently, this study provides a valuable perspective which should encourage further nutritional research in chimpanzees. Furthermore, these

results support the observation that sanctuary chimpanzees may provide a more suitable, whilst still accessible, alternative to zoological or research populations for the investigation of life history characteristics in this species.

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