December 2022

Stress and Parity Among Female Vervet Monkeys (Chlorocebus Pygerythrus) at Two Sites in South Africa

Jo Gansemer
University of Wisconsin-Milwaukee

Recommended Citation

Gansemer, Jo, "Stress and Parity Among Female Vervet Monkeys (Chlorocebus Pygerythrus) at Two Sites in South Africa" (2022). *Theses and Dissertations*. 3001.
https://dc.uwm.edu/etd/3001

STRESS AND PARITY AMONG FEMALE VERVET MONKEYS (*CHLOROCEBUS PYGERYTHRUS*) AT TWO SITES IN SOUTH AFRICA

by

Jo Gansemer

A Thesis Submitted in

Partial Fulfillment of the

Requirements for the Degree of

Master of Science

in Anthropology

at

The University of Wisconsin – Milwaukee

December 2022

ABSTRACT

STRESS AND PARITY AMONG FEMALE VERVET MONKEYS (*CHLOROCEBUS PYGERYTHRUS*) AT TWO SITES IN SOUTH AFRICA

by

Jo Gansemer

The University of Wisconsin – Milwaukee, 2022
Under the Supervision of Professor Trudy Turner

This thesis examines the hypothesis that in both Soetdoring and !Gariep populations, a female South African vervet's parity status (nulliparous or parous) affects her physiological stress levels. Vervet monkey ecology and life history are examined to contextualize the relationship between stress and parity. The testing of this hypothesis involves the analysis of hair cortisol concentrations (HCC) of samples from nulliparous and multiparous adult females of the two different South African sites. The HCC was statistically analyzed to look for correlations between stress, parity status, and site. No significant relationship between stress and parity status was found. However, significant relationships were found between stress and population site and between weight and population site.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

My profound gratitude goes out to Dr. Trudy Turner for all of her guidance and support throughout this process, especially in light of the challenges presented by COVID-19 university closures, funding issues, travel restrictions, and lab delays. I am indebted to her in light of her resiliency and for access to Vervet Project hair samples. To my other committee members, Dr. Chris Schmitt and Dr. Emily Middleton, I am grateful for their feedback and support throughout the writing of this thesis. My thanks also to Dr. Amita Kapoor and the entire Assay Services team at the Wisconsin National Primate Research Center.

To all of my professors and role models, I am eternally grateful. For all my fellow Anthropology students, and for all my friends these past few years, Mat, Rachel, Abi, Nick, Tania, Matthew, Mikayla, and, of course, Megan, it has been an honor to share this with them all. I am than thankful beyond words for their love and support, and keeping me as sane as could be managed during this process.

Finally, to my family, who have been my safe haven. To Kovu, my love and thanks for his keeping me on a schedule, and for somehow taking on almost as much stress as I had. His efforts are noted and eternally appreciated. To my wonderful wife, Bekah, I cannot express my eternal gratitude to her love, support, and guidance, unwavering no matter any obstacles in my path. I only hope to be half as supportive throughout her own thesis process.

CHAPTER 1: INTRODUCTION

Pregnancy and motherhood are critical stages in the life history of a female vervet monkey, with her parity status as an important variable at these stages. Parity stages are nulliparous, or never having given birth, primiparous, or having given birth once, and multiparous, having given birth more than one time. The pregnancy and maternal care by a monkey's dam are a driving influence on the life of the offspring, and stressors on a female can influence her maternal behavior, indirectly affecting her offspring (Carrera et al. 2020, Dettmer et al. 2015, Hinde et al. 2015, Kapoor et al. 2014). Stress, particularly chronic stress, is one source of the creation of cortisol, a hormone that has wide-reaching, and potentially negative, impacts on a vervet's life, including on its health, reproduction, survival probability, and behavior (Beehner & Bergman 2017, Dettmer et al. 2012, Grant et al. 2016, Heimbürge et al. 2019, Rakotoniaina 2017, Uno et al. 1989). The parity status of the dam may affect the stress levels that she is exposed to, as different stressors affect females of different parity statuses (Carrera et al. 2020, Dettmer et al. 2015, Mitchell & Stevens 1968). Measurements of long-term stress have been analyzed through hair cortisol (Beehner & Bergman 2017, Davenport et al. 2006, Dettmer et al. 2012, Heimbürge et al. 2019, Novak et al. 2013, Uno et al. 1989). These measurements can be useful in the care of captive vervet monkeys and in the study of both captive and wild populations by the creation of retrospective calendars of stressful periods for caretakers to utilize in stress monitoring and management or as a tool for measuring animals' physiological responses to environmental disturbances (Busch & Hayward 2009, Carlitz et al. 2014, Carlitz et al. 2016). In some populations, these stress estimates have been useful in analyzing both maternal behavior in response to stressors and offspring growth and development as affected by the dam’s cortisol they are exposed to in gestation and lactation (Carrera et al. 2020, Dettmer et al. 2009, Dettmer et al. 2018, Laudenslager et al. 2012, Saltzman & Abbott 2009, Saltzman & Abbot 2011). This research investigates the potential correlation between parity and stress, positing that in these populations, a vervet monkey’s parity status affects the levels of chronic stress she experiences.

CHAPTER 2: STRESS AND CORTISOL

Introduction

Stress is categorized as any interruption to an animal's regular physiology or behavior by exposure to a stressor, such as food insecurity, predation, parasitism or disease, aggression, or environmental change (Novak et al. 2013). Stress, particularly long-term stress, can impact an animal's overall well-being, reproductive health, and survival probability. Therefore, any accurate measurement of stress levels can be useful for ensuring and managing welfare in animal husbandry and in both behavioral and medical research efforts by establishing baseline levels as well as physiological responses to stressors that can be used to manage or mitigate stress.

Stressors

Primates in the wild may be exposed to numerous stressors. Food scarcity, predators, illness, interpersonal and intergroup aggression, and environmental change are all common examples of primate stressors (Novak et al. 2013). Anthropogenic stressors have increased with expansions in agriculture, mining, and logging, as well as with climate change (Carlitz et al. 2016, Estrada et al. 2017). These anthropogenic activities may exacerbate stressors such as habitat loss and fragmentation, predation, and disease. In addition, contact with humans and environmental changes may qualify as stressors in their own right. Physiological stress responses have been recorded in habituated primates upon contact with humans in ecotourism contexts (Setchell et al. 2017). Environmental changes such as temperature and precipitation have been found to impact stress levels in primates even before food sources are affected (Kamilar & Beaudrot 2018). Other known stressors for primates include high population density (Dettmer et al. 2014), relocation (Dettmer et al. 2012, Yamanashi 2018), social introductions (Mitchell & Stevens 1968, Yamanashi 2018), and both low and high social rank (Abbott et al. 2003, Carrera et al. 2020, Qin et al. 2013). Stressors may be immediate or chronic, and multiple stressors may affect an animal at once.

Females of different parity statuses may also experience different types of stressors, or respond variably to these stressors. For example, parous and nulliparous females have unique stressors. Nulliparous females may experience stressors in the forms of inexperience around and increased frequency of social and mating interactions with males. These are often less prevalent in older females and parous mothers who have not yet weaned their infants (Fairbanks & McGuire 1987, Schwegel et al. 2022). Some nulliparous females also face physiological stress as a result of the demands of growth, not reaching their full adult size until up to two years after reaching sexual maturity (Fairbanks 2002). On the other hand, parous females, while pregnant or nursing, experience a heightened nutritional stress that their peers do not experience. They must consume enough calories and nutrients to sustain not only themselves, but also their gestational or nursing offspring (Hauser 1994, Lee 1987). Primiparous mothers nurse more frequently than multiparous monkeys, possibly due to the body's initial inability to produce large enough quantities of milk (Gomiendo 1989). This higher frequency of nursing creates a higher degree of nutritional stress on the body in primiparous mothers.

In an early study of captive rhesus macaques, primiparous mothers were also found to react with significantly more visible stress reactions than multiparous mothers to the same social stressors (Mitchell and Stevens 1968). Vervet mothers have been observed in the wild to be more watchful over and in greater physical contact with their first offspring than with subsequent ones (Fairbanks 1988). Primiparous mothers' lack of maternal experience may lead to a higher degree of protectiveness of their offspring, and to higher levels of long-term stress for the duration of that offspring's infancy and juvenility. Nulliparous females' unique stressors are often associated with youth, such as the physiological stressor of growth and the social stressors of increased contact with males (Fairbanks 2002, Wallen & Zehr 2004).

The HPA Axis

When exposed to a stressor, an animal experiences stress, a loosely defined term for the biochemical process that occurs in the hypothalamic-pituitary-adrenocortical (HPA) axis. Stressors activate the HPA axis to produce glucocorticoid hormones (GCs) that induce homeostasis in physiological processes such as energy metabolism and neurobiological function (Grant et al. 2016, Heimbürge et al. 2019). These GCs are produced in all three of the major components of the HPA axis: 1) the hypothalamus, which synthesizes corticotropin-releasing hormones that trigger in 2) the anterior pituitary the release of adrenocorticotropic hormones that stimulate in 3) the adrenal cortex the production of GCs, including cortisol (Heimbürge et al. 2019). Cortisol is the main GC produced by this process in mammals, and has regulatory functions useful in responding to stressors, such as mobilizing energy stores, suppressing immune reactions, and regulating neurobiological functioning (Heimbürge et al. 2019, Novak et al. 2013).

Chronic Stress

Though the process of cortisol production is advantageous in mediating the immediate effects that a stressor has on an animal, it becomes more problematic in cases of long-term stress. The HPA axis continues to produce GCs in the same way as a response to immediate stressors and to long-term exposure to stressors. This exposes the animal to cortisol for extended periods of time and in increased quantities (Novak et al. 2013, Rakotoniaina et al. 2017). This extent of cortisol exposure can have a wide array of negative effects on an animal's well-being. High levels of cortisol have been found to reduce survival probabilities and to lower levels of reproductive success (Rakotoniaina et al. 2017). Chronic stress has been found to be a reliable predictor of an increased vulnerability to disease, due to its suppression of immune reactions (Qin et al. 2013). Extended exposure to cortisol has even been associated with neural degeneration in the hippocampus, exacerbating both the rate and severity of the neural damage that occurs in aging (Uno et al. 1989). Though the production of cortisol occurs to mitigate the negative effects of a stressor, in cases of chronic stress, cortisol can prove harmful or even fatal to the animal.

In the case of pregnant or nursing females, the risks of increased and prolonged exposure to cortisol affect not only the dam, but her offspring as well. The cortisol produced by the dam during pregnancy affects the infant's GC levels (Kapoor et al. 2014). Cortisol that the dam produces during lactation infuses the milk and is then ingested by the nursing offspring, also affecting its own levels (Dettmer et al. 2009, Dettmer et al. 2015, Hinde et al. 2015). The infant's chronic exposure to the dam's cortisol may impact the infant for long after the cessation of exposure, even for the offspring's entire life. These high levels of cortisol that occur prenatally and in the infancy stage have been linked to a wide array of detrimental effects in primates, including lower object permanency in infancy and impaired cognitive function into maturity (Dettmer et al. 2009). Cortisol levels have also been negatively correlated with the scores of infants in sensorimotor skill tests (Dettmer et al. 2015). The health and development of the infant are directly threatened by the dam's chronic stress due to suppressed immune responses and the diverting of energy away from growth in infancy, and the impaired maturation of organ systems during gestation (Heimbürge et al. 2019). Additionally, GCs consumed during nursing have been tied to behavioral phenotype, with high levels of cortisol in the milk leading to high irritability, low impulsivity, and a high frequency of play (Dettmer et al. 2015, Dettmer et al. 2018, Hinde et al. 2015). Therefore, the stress levels of the dam can have a direct impact on the social, neurological, and physiological development of her offspring.

Stress impacts the dam's health and behavior, including her maternal behavior. Both immediate and chronic stress can increase rates of infant abuse (Maestripieri 2011, Saltzman & Maestripieri 2011). In cases of chronic stress, common marmosets carried their infants less often than their less stressed peers, but also inspected their infants more often after they were threatened (Saltzman & Abbott 2009). High cortisol levels impair primate maternal behavior in seemingly contradictory ways by simultaneously increasing the risk of abusive and neglectful behaviors and increasing the frequency of protective behaviors. Measurements of maternal stress could therefore be useful in understanding maternal behavior and infant development.

Alhough we know that parity and stress both affect vervet monkeys' maternal behavior, it is less clear how stress and parity interact. There is considerable ongoing debate over whether or not primiparity increases cortisol concentrations. Results have varied by study in different taxa and populations. Although more studies than not have found higher GC profiles in parous primates with lower parity, the extent of these differences from multiparous females' hormone levels can greatly vary (Dettmer et al. 2015, Garber et al. 2020, Grant et al. 2016, Heimbürge et al. 2019, Hinde et al. 2015). Any significant influence of parity status on cortisol concentrations would be relevant in further understanding and studying the relationship between stress and maternity as a whole.

Hair Cortisol Concentration (HCC)

Historically, cortisol has been measured from samples of feces, urine, saliva, or blood (Heimbürge et al. 2019, Novak et al. 2013). These are vital matrices for the analysis of cortisol in acute stress, as the result of an immediate stressor. However, these analyses reflect only a timespan of a few minutes to a day or two before the sample was taken, making them less useful for estimating chronic stress (Heimbürge et al. 2019). These matrices also have the drawbacks of being affected by the time of day the sample was taken, as well as any stress that the method of sampling may have induced (Novak et al. 2013). Measuring cortisol levels from hair is not affected by these immediate stressors, and is much more advantageous in the estimation of chronic stress, as it reflects stabilized stress levels over a period of month or years (Heimbürge et al. 2019). The use of hair samples for cortisol measurements is also beneficial in its collection method. It is minimally invasive, involving only the plucking or shaving of the hair. The animal need not be anesthetized, and may be immediately released, limiting the stress placed on the animal during collection (Heimbürge et al. 2019, Novak et al. 2013).

How exactly cortisol enters the hair is not yet fully understood, although it is known that it is incorporated through the bloodstream (Heimbürge et al. 2019, Novak et al. 2013). Hair grows in a cycle of three different phases: 1) anagen, the phase of active growth, 2) catagen, the transitional phase, and 3) telogen, the resting phase (Heimbürge et al. 2019). After the completion of the telogen phase, the cycle begins again with another anagen phase. It is during this period of active hair growth that cortisol diffuses into the follicle via blood vessels (Novak et al. 2013). The cortisol becomes incorporated into the hair shaft, and remains stable over extended periods of time, even up to years after its anagen phase infusion (Heimbürge et al. 2019). Though the process by which cortisol occurs in the hair has not yet been thoroughly explored, HCC has been demonstrated to be a dependable measure of long-term stress.

HCC can be affected by a number of variables besides stress, many of which are dependent on the particular taxon or population. Different studies utilizing nonhuman primate HCC have found higher HCC in brighter pelage, lower HCC in washed hair, higher levels of HCC in juveniles than adults, higher levels of HCC in adults than juveniles, higher HCC in males than in females, higher HCC in females than in males, and higher HCC in the dry season than in the wet season (Dettmer et al. 2012, Garber et al. 2020, Heimbürge et al. 2019, Isbell 1995, Laudenslager et al. 2012, Novak et al. 2013, Yamanashi 2018). Hair cortisol concentration may also reflect localized stressors on the body (Novak et al. 2013). Localized pain, such as immersion in cold water for as little as one minute can be reflected in hair cortisol concentration (Sharpley et al. 2010). This wide variety of sometimes contradictory conclusions illustrate the importance of carefully interpreting, contextualizing, and characterizing the cortisol levels of a specific target population. Many factors can interact to influence cortisol levels in different ways.

CHAPTER 3: VERVET MONKEYS (*Chlorocebus pygerythrus*)

Introduction

Vervet monkeys are a species of Cercopithecine primate of the guenon tribe found naturally throughout eastern and southern Africa (Jasinska et al. 2013). They have also been transported to and have established populations in the Caribbean, and are used often in biomedical research (Jasinska et al. 2013). Vervet monkeys are listed as a species of least concern on the IUCN Red List, although their number are currently in decline (IUCN 2022). Their patchy distribution and relatively small local population sizes make them highly susceptible to human encroachment and human-driven habitat destruction and fragmentation (IUCN 2022, Jasinska et al. 2013, Turner et al. 2019b). Also contributing to their decreasing numbers is hunting by humans, both for bushmeat and as a defense against crop-raiding (IUCN 2022, Turner et al. 2019a). As reflected in their wide distribution, vervet monkeys have adapted to many environments including semidesert, grassland, swamp, and forest (Turner et al. 2019b). Their genetic diversity between

Figure 1: African distribution of *Chlorocebus pygerythrus* by country

populations is relatively low, suggesting a relatively recent divergence from other savanna monkeys with a lot of gene flow (Jasinska et al. 2013, Warren et al. 2015, Turner et al. 2016.)

Taxonomy

Vervet monkeys are members of the superfamily *Cercopithecoidea*, the Old World Monkeys, and of the subfamily *Cercopithecinae* (Butynski 2002, Grubb et al. 2003). The taxonomic classification of vervet monkeys, specifically, has long been, and continues to be, debated (Butynski 2002, Grubb et al. 2003, Jasinska et al. 2013, Turner et al. 2016, Turner et al. 2019c, Warren et al. 2015). Even the term vervet monkey has been disputed, now referring specifically to *Chlorocebus pygerythrus*, but being used historically as a catchall term synonymous with the currently accepted term savanna monkey for the genus *Chlorocebus* (Turner et al. 2019c). Vervet monkeys, like all savanna monkeys, have been previously classified within the genus *Cercopithecus*, historically synonymous with the guenon tribe, before the adoption of the separate *Chlorocebus*. Disputes regarding the status of the genus as one species with six subspecies, or as six different species, have been ongoing since even before the group was recognized as its own distinct genus (Grubb et al. 2003, Jaffe & Isbell 2011, Turner et al. 2019). For the sake of this research, vervet monkeys are considered one of six distinct species of savanna monkeys, taxonomically identified as *Chlorocebus pygerythrus*.

Morphology

As Cercopithecines, vervet monkeys have buccal pouches, more commonly referred to as cheek pouches, for food storage (Grubb et al. 2003). Vervet monkeys vary in their coloration from olive to light brown, variable by population and geographic location. The individuals from whom samples were taken for this study are from South Africa. These animals typically exhibit light brown pelage. Vervet monkeys have a noticeable band of white fur on their brow as well as similar tufts on their cheeks. Their tail tips are a different color than their bodies' pelage, ranging from a golden brown to black. Their hands and feet may be black or pink. The average adult vervet monkey has a cranial capacity of 69 cc (Bolter 2011). Adult male vervets are easily recognizable by their bright blue testes that pale with age and by their bright red penes (Cramer et al. 2013, Rodríguez et al. 2015). Vervet monkeys display a large degree of sexual dimorphism with respect to canines and to body size, with an average adult female body mass of 4.1 kg and an average male body mass of 5.5 kg in South Africa, where populations have the highest average body size but smallest degree of sexual dimorphism (Skinner & Chimimba 2005, Turner et al. 2018). Female body mass tends to vary, though, with areas of higher human impact producing heavier females than areas with less human impact (Turner et al. 2018).

Ecology

Vervet monkeys occupy a variety of habitat types in eastern and southern Africa, including swamp, semidesert, montane or tropical forest, agricultural land, and tourist parks, though they prefer wooded savanna (Kappeler et al. 2003, Turner et al. 2019b). Vervet monkeys can also be found on St. Kitts and Barbados in the Caribbean. They were brought over by humans during the slave trade and have since adapted to the tropical environment of the islands (Jasinska et al. 2013, Warren et al. 2015).

Vervet monkeys' environments tend to be limited by their access to water and sleeping trees. They spend more time terrestrially moving than other guenons, though still spend most of their time arboreally (Turner et al. 2019b). Vervet monkeys are able to thrive in fragmenting habitats due to their versatility in diet and ranging patterns, as well as their tendency to utilize forest edges (Turner et al. 2019b). A group's home range can vary in size from 13 to 178 ha, depending on the quality of the habitat and the size of the group (Cheney 1981, Cheney & Seyfarth 1981, Isbell et al. 1990). Vervet monkeys are omnivorous and will eat a large variety of foods as opportunistic scavengers. They are known to eat fruit, leaves, nuts, seeds, flowers, and insects, in addition to any human-derived foods they can find such as crops and garbage (Fourie et al. 2015, Turner et al. 2019b, 2019c). Their diet varies seasonally with food availability, as well as with their proximity to human habitats. Habitats disturbed by human activity and encroachment are an increasing reality for many vervet monkey populations, and this impacts food availability. In such environments, the foraging options, including food sourced from humans, tend to have more risks, namely human interaction, but also aviary predation in environments with less cover (Fourie et al. 2015, Loudon et al. 2014, Schmitt et al. 2020, Turner et al. 2019a).

Vervet monkeys' smaller body size in relation to other animals with overlapping home ranges makes them susceptible to predation by big cats, pythons, birds of prey, and larger monkeys. Increases in predation have been linked to loss of trees, habitat fragmentation, and global climate change (Estrada et al. 2017, Isbell 1998). Vervet monkeys are known to use threat-specific alarm calls to warn their group of nearby predator sightings (Cheney & Seyfarth 1981, Isbell 1998).

Socioecology

Vervet monkeys live in large multifemale-multimale groups, with female philopatry and male dispersal at the age of maturity. Males may move between groups several times throughout their lives, but are often found in groups with established male kin from their natal group or with males with whom they developed relationships in previous groups (Cheney & Seyfarth 1983, Pusey & Packer 1987). The size of a group can range anywhere between 10 and 40 individuals, dependent on the availability of space, food, and other habitat resources (Fourie et al. 2013, Turner et al. 2019b). When ecological changes alter resource availability, vervets have been known to separate into smaller groups with overlapping ranges, and to come back together into a cohesive social unit with ecological stabilization (Whitten 2019). Social relationships and hierarchies within the group are female-driven, and daughters inherit their mother's rank (Isbell 1998). Priority of access to food is rank-related and can enhance individual fitness, especially in females (Whitten 1983). Vervet monkeys are highly territorial, with both females and males defending their home range through vocalizations and physical altercations at borders (Cheney 1981).

Reproduction and Maternity

Vervet monkeys reach sexual maturity at an average age of 60 months for males and 48 months for females. Age at first birth tends to occur between 52 - 68 months, but varies with respect to habitat quality (Cheney et al. 1988, Fairbanks & McGuire 1987). Females with greater access to resources such as space or calorie and nutrient rich foods, tend to have a lower age at first birth than females with fewer available resources (Cheney et al. 1988, Ellis et al. 2009, Jarrett et al. 2020, Lee 1984, Ross & Jones 1999, Schmitt et al. 2020, Whitten & Turner 2009). The gestational period of vervet monkeys is about 165 days, and the interbirth interval is 12-17 months (Rowell 1970, Cheney et al. 1988). Interbirth interval is similarly impacted by habitat quality, with higher quality habitats resulting in lower interbirth intervals. Given the regular interbirth intervals, the mean age at first birth, and an estimated lifespan of up to twelve years, the average female could give birth as many as six times throughout her life.

Though female vervet monkeys are capable of breeding at a mean age of two to three years, they do not reach their full adult size until their fourth year (Fairbanks 2002, Horrocks & Hunte 2002, Whitten & Turner 2009). Males mature more slowly, typically reaching their adult size at five years, and subsequently dispersing (Fairbanks 2002, Horrocks & Hunte 2002). Vervets are typically fully weaned by two years of age, as lactation begins in pregnancy and lasts for up to 18.5 months after birth (Fairbanks 2002, Schmitt et al. 2020). Weaned monkeys are still immature and dependent on their mothers for help, including in foraging efforts (Fairbanks 2002, Hauser 1994, Lee 1984). The mother’s involvement in her offspring’s life does not end at weaning and, likewise, the offspring continues to significantly influence the mother's life long after both infancy and weaning, especially their philopatric female offspring. Given their continuously high levels of interaction, stressors that affect one may have an indirect, but nonetheless notable, effect on the other.

Vervet monkeys are unusual in mother-infant behavior in that their infants tend to be more outgoing and socially adventurous than those of other primates. Vervet infants spend less time with their mothers than other Cercopithecines, spending less time clinging to and being groomed by their dams, as well as having greater contact at earlier ages with non-caregiving adults (Struhsaker 1971). Female vervet monkeys approach their daughters and spend more time on affiliative activities, such as grooming, on them than they do on their sons (Fairbanks & McGuire 1985). Throughout juvenility, including after weaning, the offspring will learn from and model behaviors of the mother, more so in cases of high ranking mothers (Fairbanks & McGuire 1985, van de Waal et al. 2014). Maternal rejection of her offspring is uncommon, but becomes more likely under certain conditions such as low resource availability, possibly as a trade-off between sustaining the current offspring and the prioritizing dam's future reproduction (Fairbanks & McGuire 1995). Offspring rejection is also more likely in cases of maternal immaturity and inexperience, both traits associated with primiparity (Fairbanks & McGuire 1995). However, maternal inexperience can be limited in primiparous mothers who have alloparental experience caring for younger siblings or other juveniles throughout her adolescence and subadulthood (Fairbanks 1990, Johnson et al. 1980).

In addition to vervet monkeys, many other primate taxa females' maternal behavior, including the amount of time spent with their infant, is impacted by parity. Primiparous rhesus macaques have been found to be more protective of their infants, threatening and fear-grimacing at perceived threats more frequently than multiparous females. They also soothed by stroking and petting their offspring more often in response to a stressor (Mitchell & Stevens 1968). Primate dams tend to nurse their infants more frequently, and have a greater than average interbirth interval after their first birth (Gomendio 1989). Primiparous mothers tend to be more protective, with inflated rates of contact, attention, and supervision of their first infant, except in the case of an infant's death, after which a mother will be more protective of subsequent offspring (Fairbanks 1988). These behaviors illustrate that vervet dams will alter their maternal behaviors based on their previous experience as mothers, and that primiparous and multiparous mothers can react differently to stressors.

Stress, Socioecology, and Life History

Socioecological theory has traditionally posited that in a taxon, distinct types of food competition produce distinct types of social units, following the premise that male reproduction is constrained by female reproduction, which is constrained by access to food (Janson 2000, Snaith & Chapman 2007, Terborgh & Janson 1986, Thierry 2008). Since around the turn of the century, there has been debate surrounding the efficacy and longevity of the theory, as social patterns do not actually correlate directly with resource patchiness in most populations (Clutton-Brock & Janson 2012, Janson 2000, Ross & Jones 1999, Snaith & Chapman

2007, Thierry 2008). Despite the debate, socioecological theory has remained, as its general hypothesis that ecology affects social behavior is still accepted (Janson 2000, Whitten 2019). Over the past few decades, the theory has moved away from strict causative models of feeding, rejecting the premise that any one model can explain the stated hypothesis (Clutton-Brock & Janson 2012, Snaith & Chapman 2007, Thierry 2008). Additionally, the rate of anthropogenic changes to the environment has become more rapid than most long-lived animals, including vervet monkeys, can evolutionarily adapt to (Estrada et al. 2017, Kamilar & Beaudrot 2018). This has refined socioecological theory, encompassing multiple ecological factors' impacts on a variety of behaviors, on both the individual and population levels.

The increased frequency of anthropogenically altered habitats due to human encroachment, deforestation, and conversion to agricultural land may also factor into vervet monkeys' stress levels (Fourie et al. 2015, Kamilar & Beaudrot 2018, Loudon et al. 2014). The high-risk foraging options, greater risk of predation, and increased possibility of human-vervet encounters present in these altered habitats could lead to higher chronic and specific stress levels (Estrada et al. 2017, Fourie et al. 2015, Isbell 1998, Schmitt et al. 2020, Turner et al. 2019a). High-risk foraging, in particular, has been linked to increased cortisol levels in males, as males are more likely to engage in risky foraging than females, especially females with dependent offspring (Fourie et al. 2015, Schmitt et al. 2020).

Life history theory is built on describing the life history strategy that maximizes fitness; like socioecological theory, it has come to be viewed as a set of principles and trade-offs, rather than one strict model (Brommer 2000, Turner et al. 2019d). A trade-off is a negative correlation between two life history traits, such as body size and timing of maturity (Turner et al. 2019d). The timing of a taxon's life events, including birth, death, and sexual maturation, all impact survival and reproduction, so are the result of natural selection (Hill 1993). However, survival and reproduction cannot always be prioritized together, and the theory depends on the premise that energy and resources spent on one life history trait are energy and resources not spent on another. Greater growth requires more time, which limits reproductive years. More reproductive years requires an earlier age at first reproduction, which limits growth (Whitten & Turner 2009). This trade-off does not exist independently of outside factors. Ecological factors such as resource availability and habitat quality have been found to hasten the onset of sexual maturity (Cheney et al. 1988, Rowell et al. 1970, Schmitt et al. 2020, Whitten & Turner 2009). Life history strategies are not comprehensive models. In many animals, including primates, life history trade-offs are affected by a number of variables, including stress and environment, and vary not just between taxa, but between populations (Crespi et al. 2013, Ellis et al. 2009, Kamilar & Beaudrot 2018, Schultner et al. 2013, Whitten & Turner 2009).

Stress also impacts life history. Stress levels of both dam and offspring can impact the offspring's rates of growth and development, slowing or hastening them dependent on the stressor (Carrera et al. 2020, Dettmer et al. 2009, Dettmer et al. 2015, Grant et al. 2016, Hinde et al. 2015, Laudenslager et al. 2012, Petrullo et al. 2019). Stress has also been linked to decreased lifespan in primates (Rakotoniaina 2017, Uno et al. 1989). As with life history, stress has also been linked to socioecological factors. In primates, stress levels have been shown to be impacted by: social rank and relationships, in which low social rank acts as a stressor in its limiting of physical and social resources and high rank acts as a stressor in that a higher social rank usually requires maintenance and defense; food availability and quality, in that food low in nutrients or calories or a lack of food, in general, is a physiological stressor; and environmental quality, in that a lack of space, such as sleeping sites, or polluted environments acts as physiological stressors (Abbott et al. 2003, Carlitz et al. 2016, Carrera et al. 2020, Dettmer et al. 2014, Dettmer et al. 2012, Fourie et al. 2015, Garber et al. 2020, Kamilar & Beaudrot 2018, Qin et al. 2013, Sapolsky 2021, Schmitt et al. 2020).

Primate life history, socioecology, and stress are all related to one another. The timing and trade-offs of life history traits are affected by ecology and by socioecological factors. Stress levels, impacted by socioecological factors, influence life history strategies. For the research conducted here, life history and socioecology theories were both taken into consideration to best elucidate the multiple factors affecting cortisol, parity, and the possible relationship between them.

CHAPTER 4: HYPOTHESIS AND PREDICTIONS

Hypothesis

Given the interaction between life history traits, notably maternity in this research, socioecological factors including human impact on the environment, and stress levels, I propose to study the impact of parity status on chronic stress levels based on hair cortisol concentration in two South African populations of wild vervet monkey: one in Soetdoring Nature Reserve, where monkeys have few natural predators and survive primarily on natural forage, and one in !Gariep Dam where the monkeys forage foods sourced from human agriculture but experience anthropogenic stressors like hunting, snaring, and being shot. I hypothesize that in both Soetdoring Nature Reserve and !Gariep Dam, a female vervet monkey's parity status (nulliparous or multiparous) affects her physiological stress levels. With respect to this hypothesis, four predictions are explored.

Predictions

1. Parous females are predicted to have higher HCC than nulliparous females, because they may face chronic stressors that nulliparous females do not, such as nutritional stress due to lactation or pregnancy, and rearing and protecting offspring throughout nursing and after weaning (Fairbanks 1988, Fairbanks 2002, Gomiendo 1989, Hauser 1994, & Mitchell & Stevens 1968).

2. Body mass is expected to negatively correlate with HCC in parous females, as lower weight could be indicative of a greater degree of nutritional stress (Fourie et al. 2015, Hinde et al. 2015, Novak et al. 2013).
3. Age is predicted to negatively correlate with HCC in parous females, as lesser age may be indicative of less maternal experience and therefore, higher stress (Cheney et al. 1988, Fairbanks 2002, Laudenslager et al. 2012).
4. Females in !Gariep are expected to have higher HCC than females in Soetdoring, due to both riskier foraging options in a more anthropogenically impacted habitat and to earlier possible sexual maturation and parity onset due to the higher nutrient and calorie content of human-sourced foods (Cheney et al. 1988, Loudon et al. 2014, Novak et al. 2013, & Schmitt et al. 2020).

In addition to these specific predictions, all available variables (sex, weight, population site, age, parity status, lactation status, and cortisol) will be tested against one another to explore any interaction effects that were not predicted based on the background information presented.

CHAPTER 5: METHODS

Study Subjects and Sample Methods

This research looks at hair samples from South African vervet monkey females from two different sites: !Gariep Dam and Soetdoring Nature Preserve. The two sites are both located in Free State, South Africa and are of similar environment. Both sites are grasslands at a similar altitude, experiencing similar annual temperature and precipitation levels. Both populations primarily occupy riparian forest edges, thought the !Gariep Dam monkeys spend more of their time in agricultural fields, without aerial cover. The vervets of the !Gariep Dam site experience higher levels of anthropogenic interference in the form of agricultural land, spending time in that land and supplementing their diet with agricultural fields, orchards, and horse feed. The vervets of the Soetdoring Nature Preserve site experience less anthropogenic interference. They subsist primarily on natural forage with some food gotten from visitors to the preserve (Schmitt et al. 2020, Turner et al. 2018).

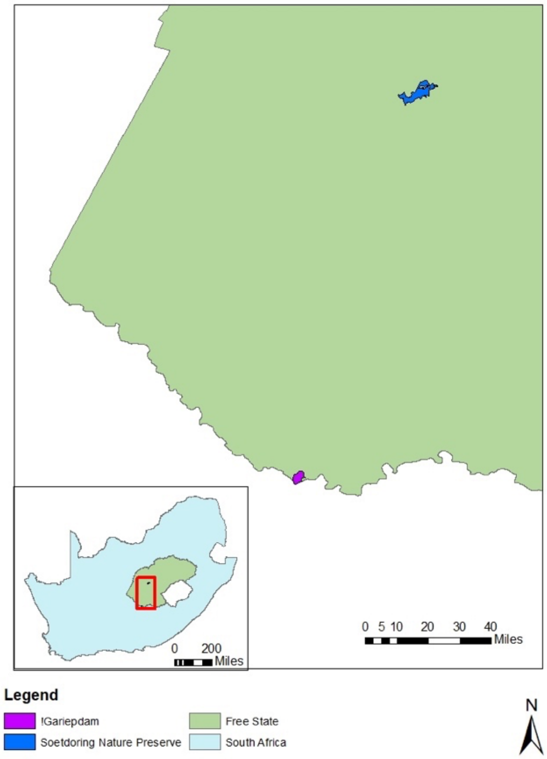


Figure 2: Study site locations with reference to Free State, South Africa

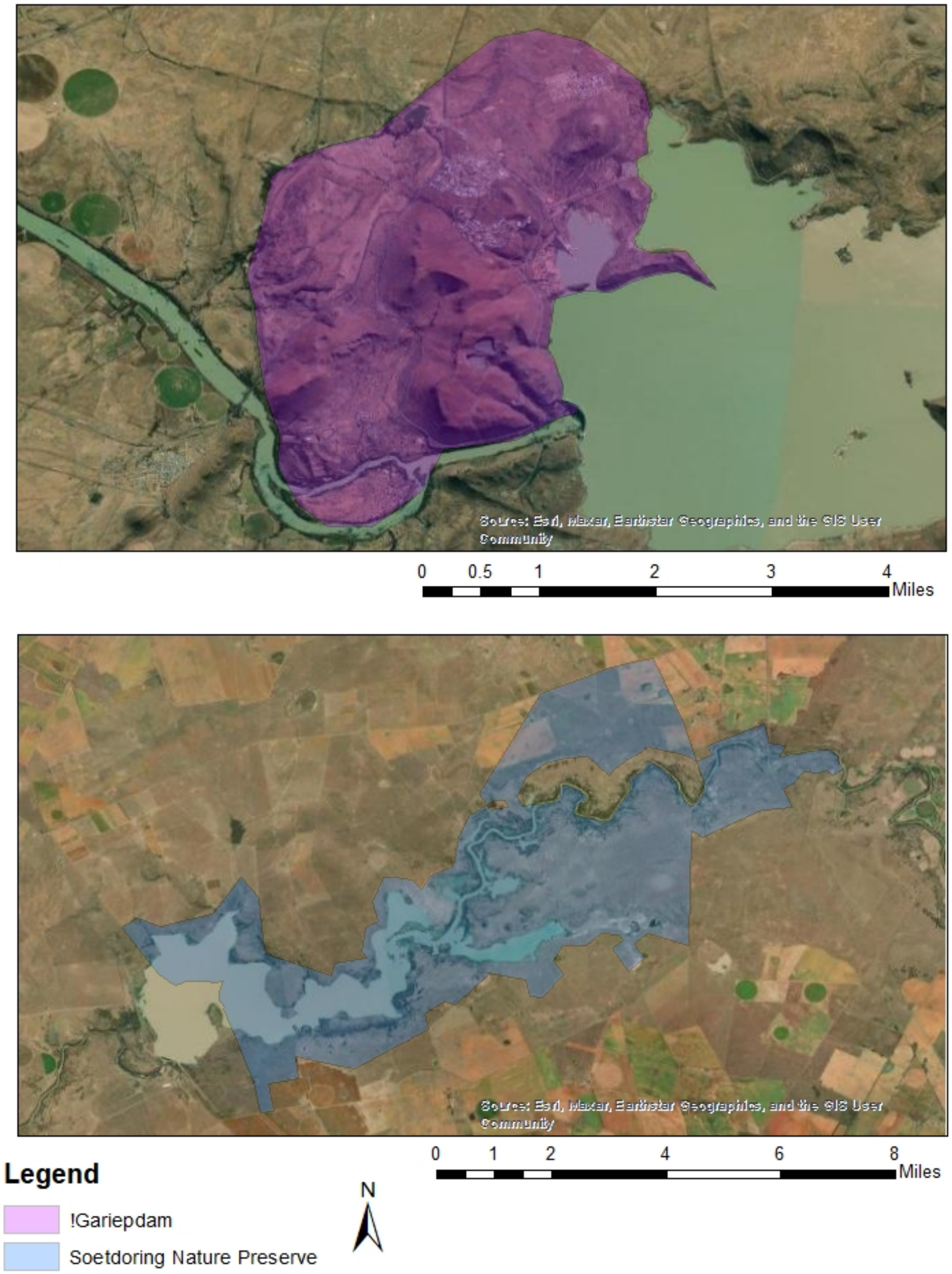
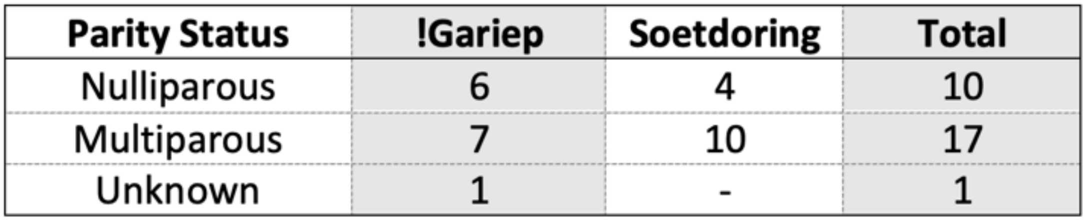


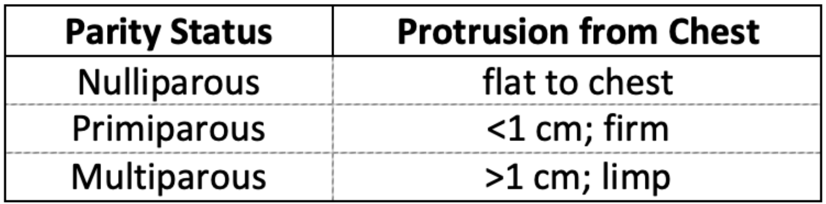
Figure 3: Aerial view of study sites

The hair samples were collected from adult females aged two to eight years based on dental estimates, with different parity statuses: nulliparous and multiparous. No females in the sample pool are primiparous. From the !Gariep site, six samples are from nulliparous females and seven samples are from multiparous females. From the Soetdoring site, four samples are nulliparous and 10 samples are multiparous. Across the sites, 10 samples are from nulliparous females and 17 samples are from multiparous females. One sample, from the !Gariep site, cannot be identified with regard to parity. Parity status was determined by nipple morphology in accordance with Turner et al. (1997), with nulliparity indicated by nipples flat to the chest, primiparity indicated by firm nipples protruding <1 cm from the chest, and multiparity indicated by limp nipples extending >1 cm from the chest. Lactation status is available for 11 of the parous females. Lactation status was determined by the presence of milk expression from the nipple in accordance with Whitten & Turner (2009).



Parity Status	!Gariep	Soetdoring	Total
Nulliparous	6	4	10
Multiparous	7	10	17
Unknown	1	-	1

Table 1: Parity status by site



Parity Status	Protrusion from Chest
Nulliparous	flat to chest
Primiparous	<1 cm; firm
Multiparous	>1 cm; limp

Table 2: Parity status determined by nipple morphology

Samples were all collected between June and August 2010, preventing any skewing of data based on seasonal changes to cortisol levels. All samples were taken from sexually mature subadult and adult females, limiting data skew based on sex or age. The animals were live trapped, baited to wood-framed, wire mesh-topped drop traps by corn, consistent with Grobler & Turner 2010. As described in Jasinska et al. 2013, the animals that were caught in traps were subsequently anesthetized by a veterinarian with 4 mg/kg of equal parts ketamine/xylazine. While anesthetized, the monkeys were measured and visually examined for age, sex, body size, morphometric measures, and parity status. Animals were each microchipped with a unique ID marker for future identification. Blood samples, fecal samples, and hair samples were collected from each individual. Hair was bagged and securely stored until analysis for HCC. All animals were released after examination, sampling, and recovery from anesthesia (Jasinska et al. 2013, Turner et al. 2018).

Sex	Population Site	Parity Status	Lactation Status	Cortisol (pg/mg)	Dental Age (years)
F	Soetdoring	Nulliparous	N/A	17.773	4
F	Soetdoring	Nulliparous	N/A	29.149	2
F	Soetdoring	Nulliparous	N/A	38.353	5
F	Soetdoring	Nulliparous	N/A	46.353	6
F	Soetdoring	Multiparous	Unknown	25.102	7
F	Soetdoring	Multiparous	Unknown	72.559	8
F	Soetdoring	Multiparous	Non-lactating	14.189	Unknown
F	Soetdoring	Multiparous	Non-lactating	20.966	8
F	Soetdoring	Multiparous	Non-lactating	25.684	7
F	Soetdoring	Multiparous	Non-lactating	32.321	7
F	Soetdoring	Multiparous	Lactating	25.945	8
F	Soetdoring	Multiparous	Lactating	45.709	7
F	Soetdoring	Multiparous	Lactating	45.717	7
F	Soetdoring	Multiparous	Lactating	92.710	8
F	!Gariep	Unknown	Unknown	7.624	7
F	!Gariep	Nulliparous	N/A	12.353	4
F	!Gariep	Nulliparous	N/A	15.914	4
F	!Gariep	Nulliparous	N/A	16.569	6
F	!Gariep	Nulliparous	N/A	22.324	6
F	!Gariep	Nulliparous	N/A	33.710	3
F	!Gariep	Nulliparous	N/A	33.984	6
F	!Gariep	Multiparous	Unknown	3.770	7

F	!Gariep	Multiparous	Unknown	21.718	Unknown
F	!Gariep	Multiparous	Unknown	25.146	8
F	!Gariep	Multiparous	Unknown	26.741	Unknown
F	!Gariep	Multiparous	Lactating	18.359	8
F	!Gariep	Multiparous	Lactating	30.792	8
F	!Gariep	Multiparous	Lactating	32.906	7
M	Soetdoring	N/A	N/A	12.464	5
M	Soetdoring	N/A	N/A	13.563	7
M	Soetdoring	N/A	N/A	14.175	8
M	Soetdoring	N/A	N/A	31.238	2
M	Soetdoring	N/A	N/A	40.020	5
M	Soetdoring	N/A	N/A	51.810	7
M	!Gariep	N/A	N/A	7.221	7
M	!Gariep	N/A	N/A	9.190	7
M	!Gariep	N/A	N/A	10.165	7
M	!Gariep	N/A	N/A	10.401	6
M	!Gariep	N/A	N/A	19.941	5
M	!Gariep	N/A	N/A	21.109	5

Table 3: All sampled animals

HCC Analysis

Hair samples were transported to the Wisconsin National Primate Research Center (WNPRC) for HCC analysis. Analysis was performed by WNPRC Assay Services, under the supervision of Unit Head Dr. Amita Kapoor. Hair cortisol analysis is based on the shaft of the hair, which is well-associated with blood cortisol levels (Davenport et al. 2006, Novak et al. 2013). Consistent with Kapoor et al. (2014), the hair samples were washed by combining with 2-propenol and vortexing. 2 ml 2-propenol is then collected to determine the level of steroid loss before the hair goes through a second wash cycle, after which another 2 ml of 2-propenol is collected. The hair is then dried under a stream of air. The dried hair is ground into a fine powder before extraction. The extraction combines powdered hair with methanol, Sorenson buffer, and the internal standard. The sample is incubated at 30 degrees for 16 hours. After incubation, samples are vortexed and centrifuged to collect the supernatant. The supernatant is then run through both solid-phase and liquid-phase extractions. The samples were then analyzed on a mass spectrometer utilizing high-pressure liquid chromatography-tandem mass spectrometry. This allows for the detection and measurement of up to eight different steroids, including cortisol.

Statistical Analysis

I performed all statistical analysis in RStudio 2022.02.3.492 (R Core Team 2022). Figures were plotted using package ggplot2 v3.3.6 (Wickham et al. 2016). I tested each relationship in the four predictions using ordinary least squares (OLS) linear regression or multiple regression with HCC (pg/mg) as the response variable. In prediction 1, I used parity status (nulliparous or parous) as the predictor, or independent, variable, which does not depend on other variables to provide its value, and instead alters the dependent variable, cortisol. HCC is expected to be greater in the parous condition. In prediction 2, I expected HCC to negatively correlate with body mass in parous females, using weight (kg) and parity status as predictor variables. In prediction 3, I expected HCC to be higher in younger females, particularly in younger parous females than in older parous females. I used age in dental years and parity status as predictor variables. In prediction 4, I used population (!Gariep or Soetdoring) as the predictor variable, and HCC is expected to be greater in females of the !Gariep population. I also used multiple regression to explore the relationships between all different variables and their interaction effects, or the effect that each predictor variable has, with respect to other predictor variables, on the dependent variable. In order to choose the most effective formula, which is the simplest, with the least possible variables, and has the most predictive power, I used subset selection. Subset selection is used to find the specific combination of all possible combinations of predictor variables that provided the highest adjusted r^2 value.

CHAPTER 6: RESULTS

Prediction 1

My prediction that parous females would have higher HCC than nulliparous females was unsupported (p = 0.401; adjusted r^2 = -0.010; Figure 4), indicating that parity status alone is not a good predictor of HCC. Removing the outliers from dataset did not change this result (p = 1; adjusted r^2 = -0.056; Figure 5). Although the outlying females of known age were are at least six years old based on dental estimates, dental age was also not significantly correlated with HCC, either on its own (p = 0.192; adjusted r^2 = 0.034) or in conjunction with parity status (p = 0.436; adjusted r^2 = -0.012).

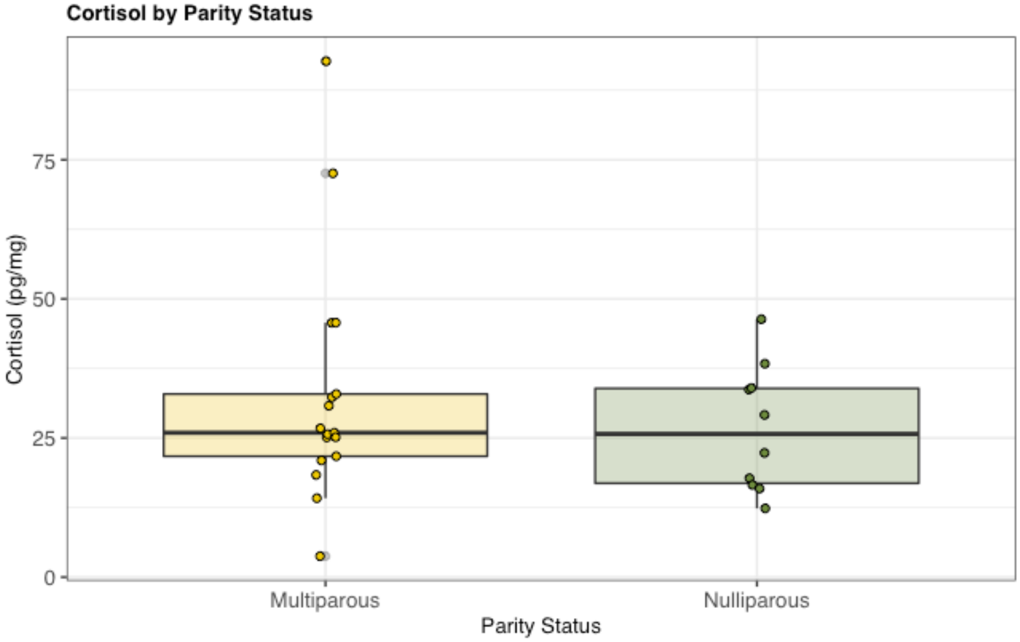


Figure 4: Boxplot of HCC as a function of parity status

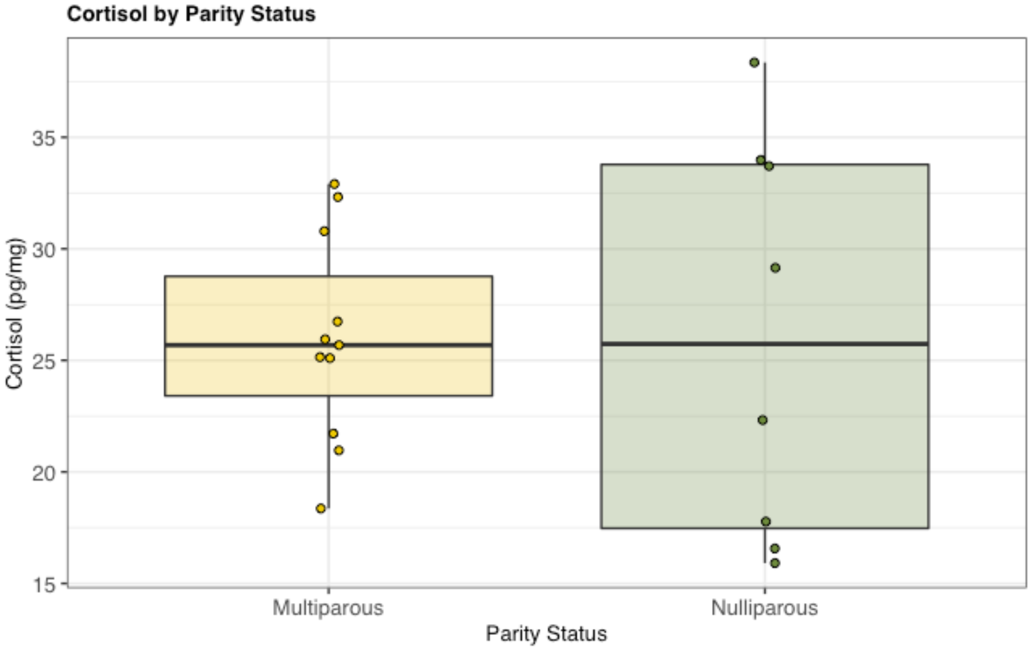


Figure 5: Boxplot of HCC as a function of parity status with outlying cortisol values removed

Prediction 2

My second prediction, which stated that body mass was expected to negatively correlate with HCC in females, was also unsupported ($p = 0.604$; adjusted $r^2 = -0.029$; Figure 6). Removing the outlying cortisol values from the dataset did not change this result ($p = 0.815$; adjusted $^{r2} = -0.055$; Figure 7). More specifically, my prediction that body mass was expected to negatively correlate with HCC in parous females was unsupported ($p = 0.895$; adjusted $r^2 = -0.082$). HCC as a function of both body mass and parity status also showed no significant correlation ($p = 0.691$; adjusted $r^2 = -0.050$), although body mass and parity status were significantly correlated with each other ($p < 0.001$; adjusted $r^2 = 0.597$; Figure 8). Controlling for age by excluding the subadult females did not change this result ($p < 0.001$; adjusted $r^2 = 0.529$). Body mass was also significantly associated with both parity status and population together ($p < 0.001$; adjusted $r^2 = 0.729$; Figure 9). Body mass and dental age are also positively correlated in both populations ($p < 0.001$; adjusted $r^2 = 0.644$).

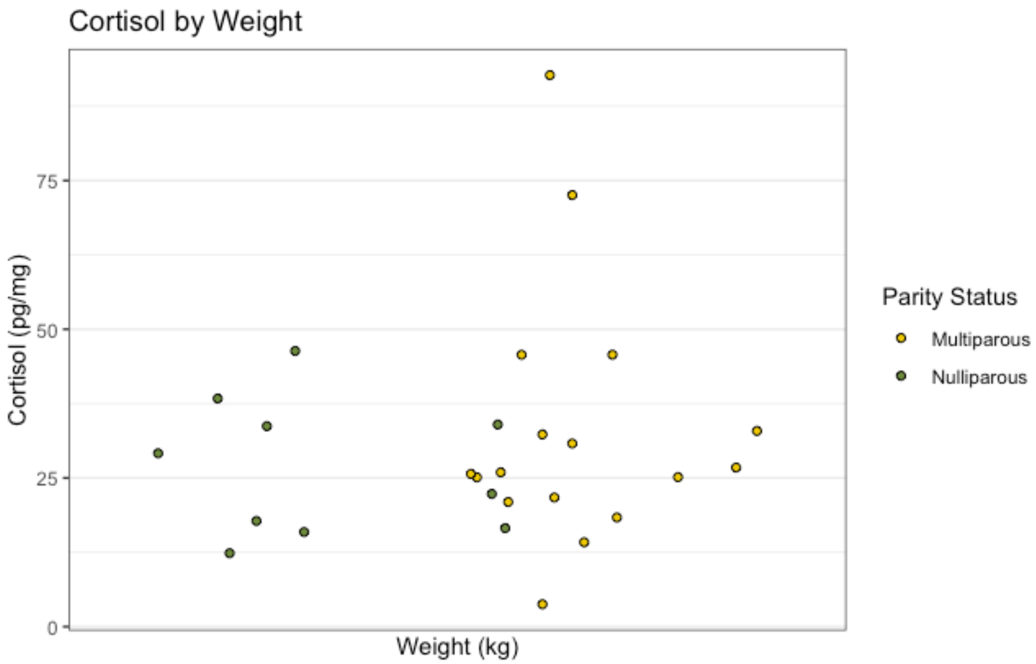


Figure 6: Scatterplot of HCC as a function of weight

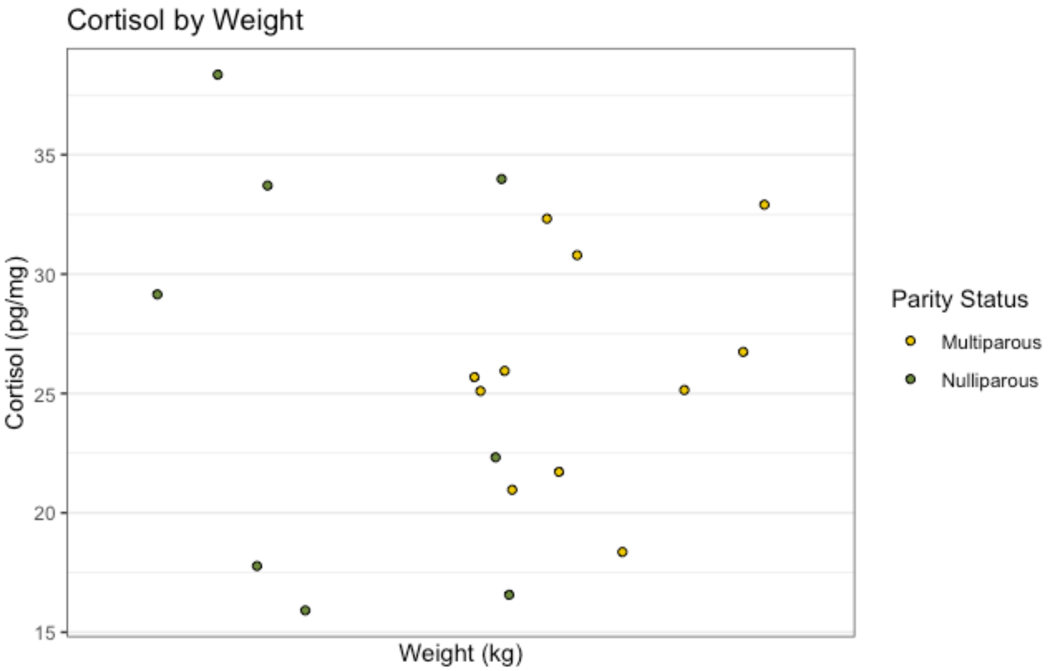


Figure 7: Scatterplot of HCC as a function of weight with outlying cortisol values removed

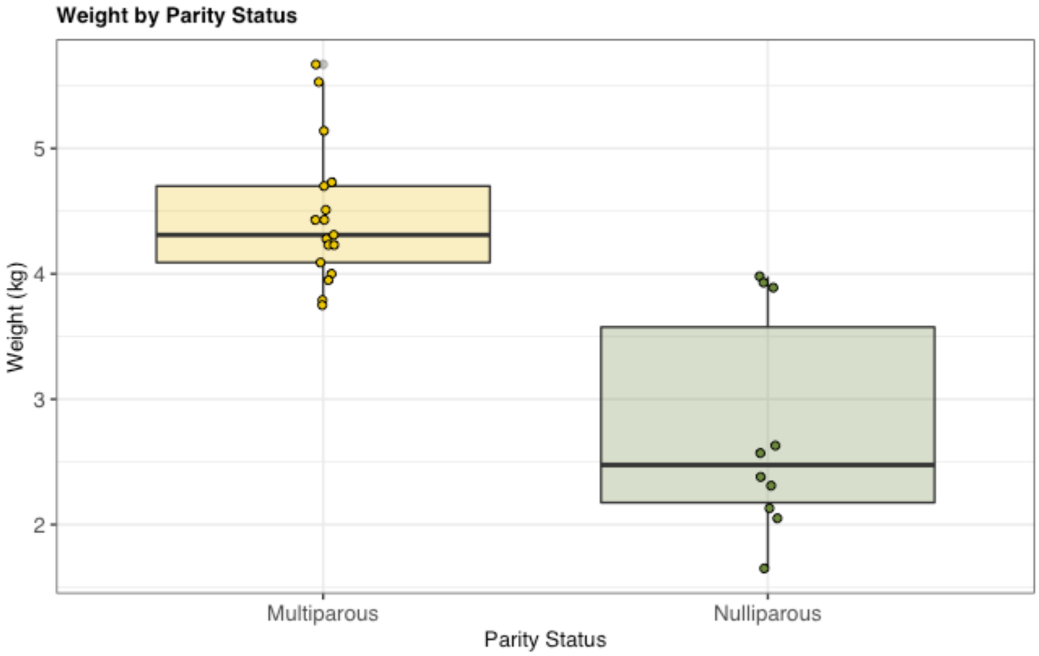


Figure 8: Boxplot of weight as a function of parity status

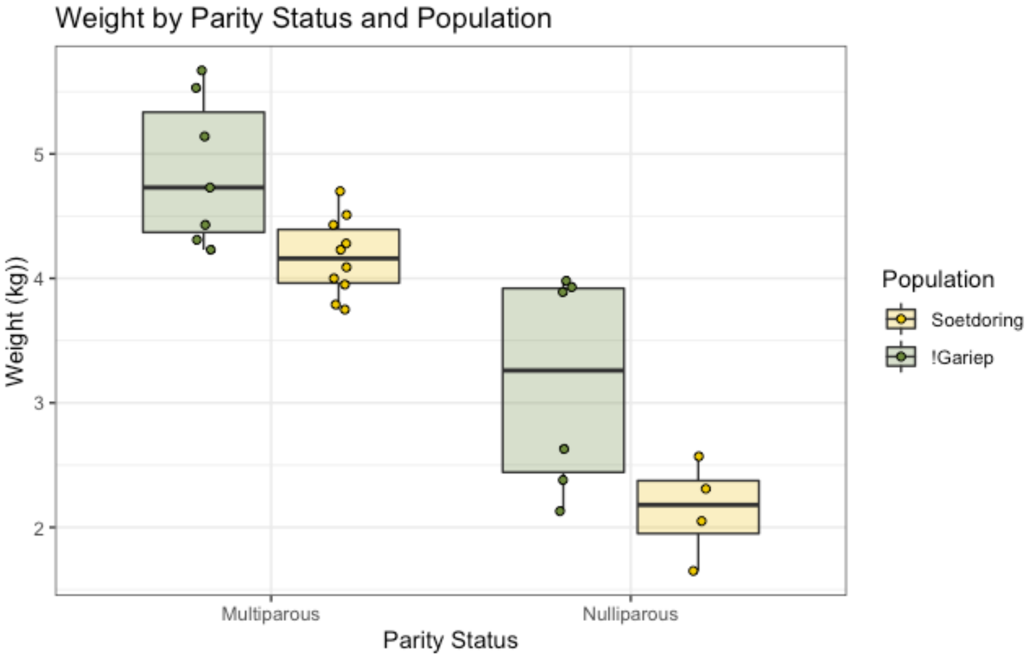


Figure 9: Boxplot of weight as a function of parity status, split by population

Prediction 3

My prediction that age alone would have a negative relationship with HCC was not supported ($p = 0.751$; adjusted $r^2 = -0.059$; Figure 10). More specifically, my prediction that age was expected to negatively correlate with HCC in parous females was also unsupported ($p = 0.401$; adjusted $r^2 = -0.019$).There was no significance in the relationship between HCC and age in the females, even when split by population (In Soetdoring: $p = 0.739$; adjusted $r^2 = -0.144$; In !Gariep: $p = 0.524$; adjusted $r^2 = -0.033$). Age and HCC also did not correlate in the entirety of the population, even when the males were included ($p = 0.413$; adjusted $r^2 = -0.009$).

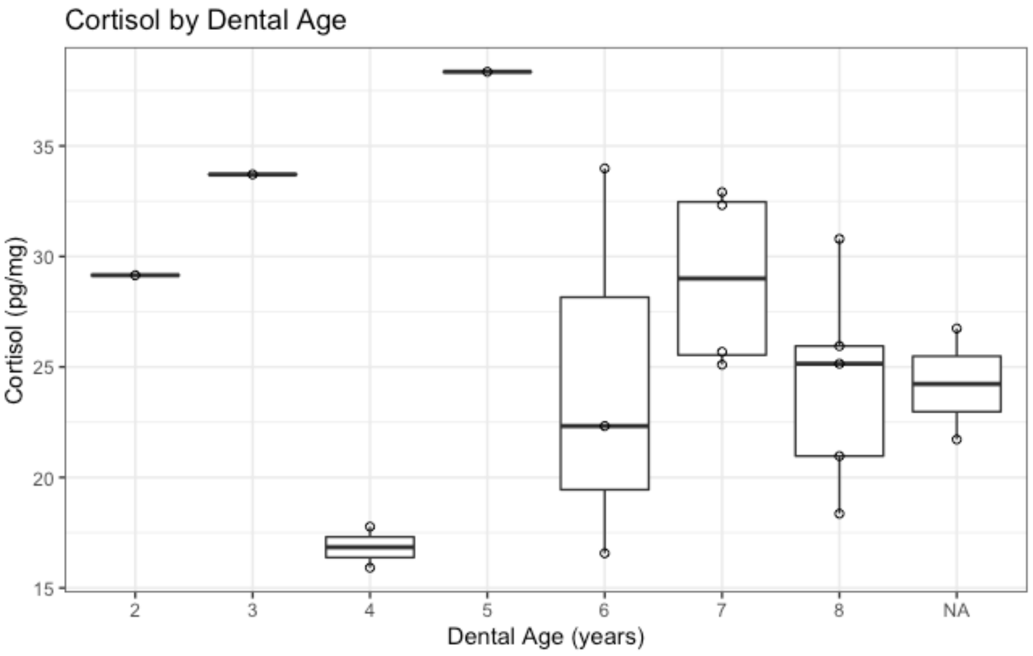


Figure 10: Boxplot of the females' HCC as a function of dental age

Prediction 4

My final prediction, that the !Gariep females would have higher average HCC than the Soetdoring females, was not supported ($p = 0.608$; adjusted $r^2 = -0.042$; Figure 11). HCC was found to have a significant relationship with population when both the male and the female vervets were included in the data (p = 0.004; adjusted r^2 = 0.182; Figure 12). With outlying cortisol values removed, the model ceases to be statistically significant (p = 0.164; adjusted r^2 = 0.047; Figure 13). Males alone, like females alone, do not have a significant relationship in their population site and cortisol levels (p = 0.075; adjusted r^2 = 0.211; Figure 14).

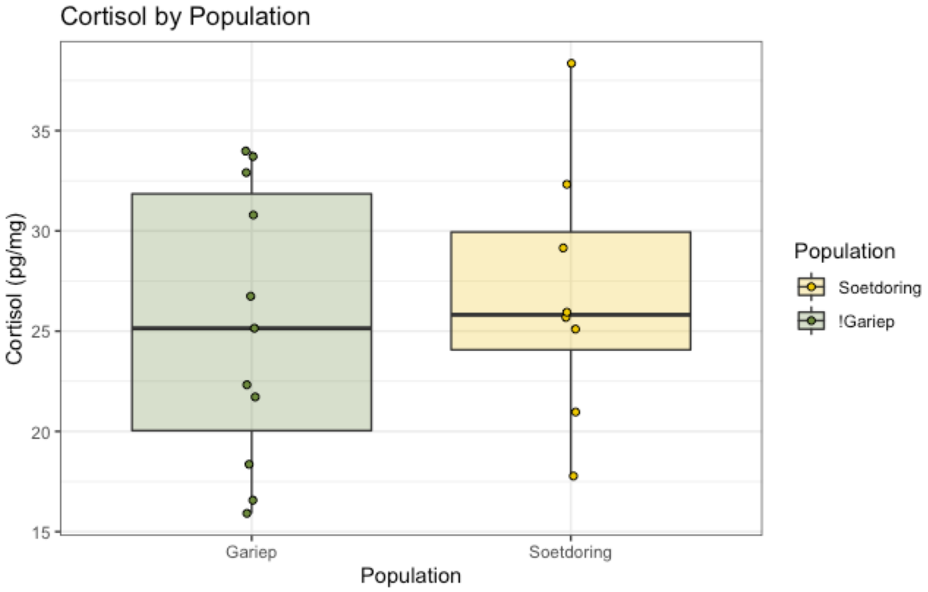


Figure 11: Boxplot of HCC as a function of population

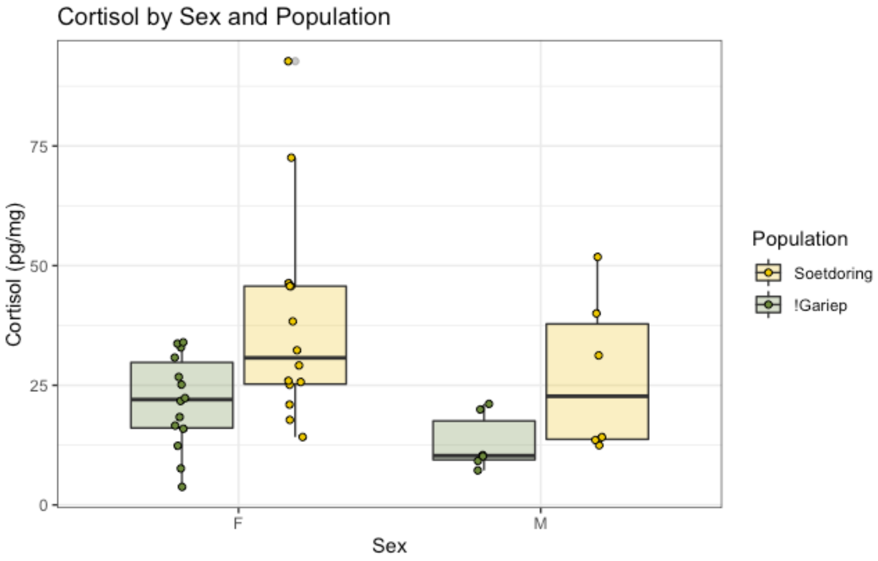


Figure 12: Boxplot of HCC as a function of population, split by sex

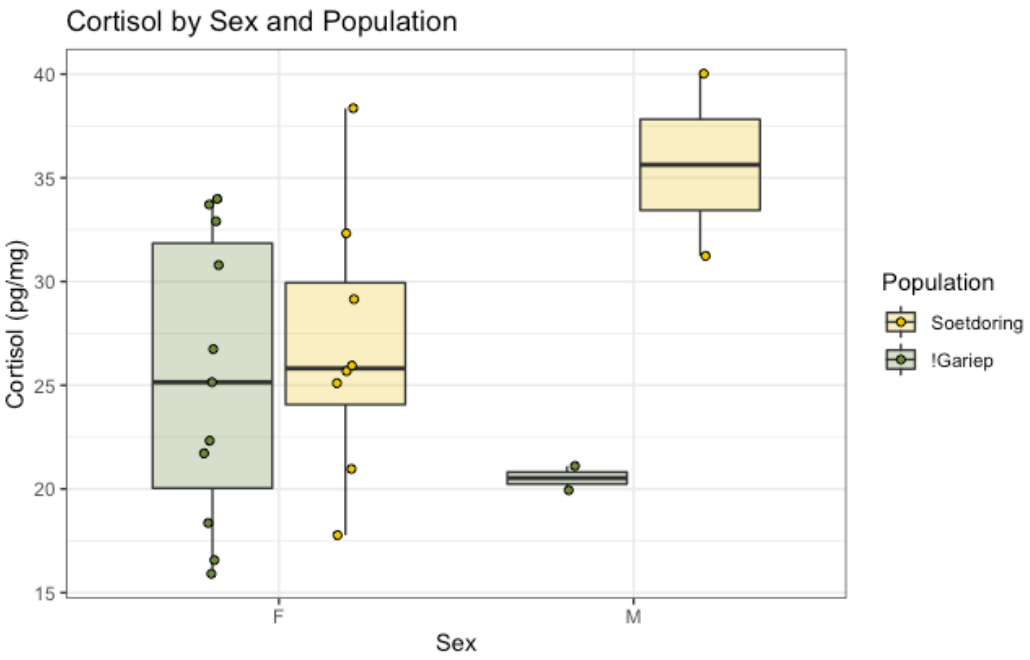


Figure 13: Boxplot of HCC as a function of population with outlying cortisol values removed, split by sex

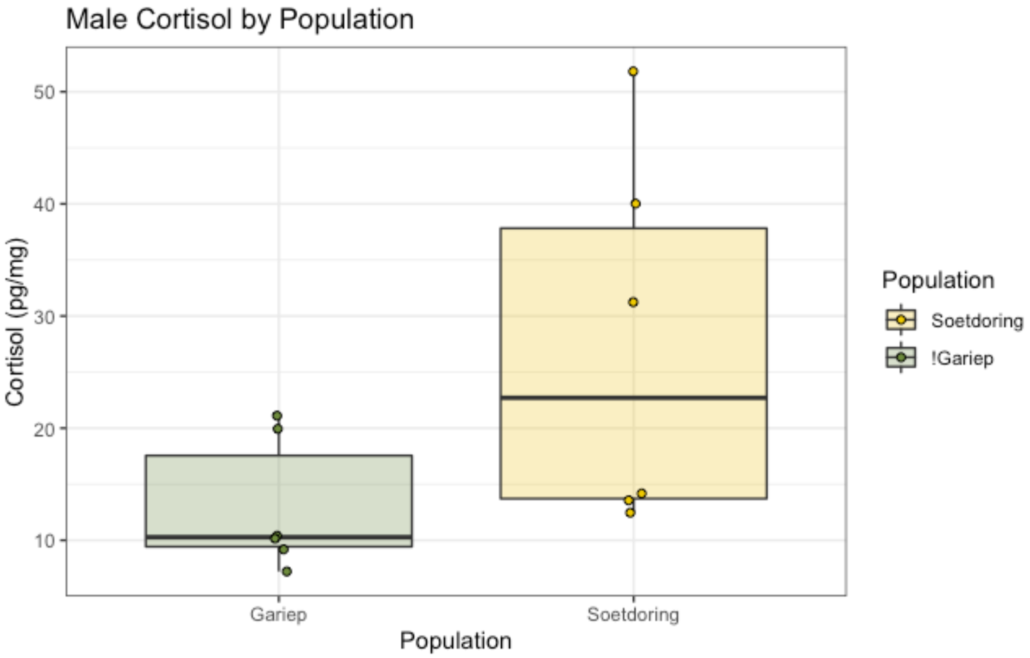


Figure 14: Boxplot of HCC as a function of population in males

Other

In addition to the four specific predictions, I tested the relationship between cortisol and all other variables by using cortisol as the response variable and sex, dental age, weight, population site, parity status, and lactation status as the predictor variables without interaction effects, which proved significant ($p = 0.03$; adjusted $r^2 = 0.267$). Also significant was the inclusion of interaction effects ($p = 0.018$; adjusted $r^2 = 0.797$). I used subset selection, the successive running of each possible equation using all combinations of the six variables, to find the best of the 64 possible models. The number of possible models is every combination of the dependent variable (cortisol), calculated by one, two, three, four, five, and all six variables (calculable with 2^n, were n is the number of predictor variables). The five predictor model proved to be the best, with the highest adjusted r^2, the same p-value and adjusted r^2 as the full model with all six predictors, and being simpler in that one less variable was included. No significant interaction effects, other than those documented above in Prediction 2, were observed.

CHAPTER 7: DISCUSSION

Analysis of Results

None of my four predictions were specifically supported by the results. My first prediction, that parous females would have higher HCC than nulliparous females, was unsupported. There was no direct correlation between HCC and parity at all. My prediction that HCC and body mass would be negatively correlated was also unsupported, suggesting that body mass, alone, is not a good predictor of HCC. HCC as a function of both body mass and parity status also showed no correlation. Body mass and parity status were significantly correlated with each other, however. Multiparous females weighed significantly more than nulliparous females, with multiparous females having a mean weight of 4.46 kg and nulliparous females having a mean weight of 2.75 kg. Body mass was also significantly associated with both parity status and population together. Nulliparous females at Soetdoring weigh the least on average (mean = 2.15 kg), while multiparous females at !Gariep weigh the most on average (mean = 4.86 kg). This is likely because multiparous females in many species and populations weigh more than nulliparous females due to the excess weight associated with pregnancy and lactation (Fairbanks & McGuire 1995, Gomiendo 1989, Lee 1987). Body mass and dental age are also correlated in both populations, but the correlation between body mass and parity is not age related, as removing subadult females from the sample did not negate the relationship. Instead, body mass may be more affected by diet, as the !Gariep females have the highest average weight. That additional weight may be a result of

Parity Status	!Gariep	Soetdoring
Nulliparous	3.16	2.15
Multiparous	4.86	4.17

Table 4: Mean weight (kg) by parity status and population site

the additional foraging and human-sourced food supplies, including crops, which are higher in calories and nutrients (Ellis et al. 2009, Jarrett et al. 2020, Lee 1987, Ross & Jones 1999, Schmitt et al. 2020).

My third prediction, that age alone would have a negative relationship with HCC in parous females, was not supported, either. This prediction was based on the premise that, in parous females, youth is associated with maternal inexperience and immaturity (Fairbanks 1988, Fairbanks & McGuire 1995, Maestripieri 2011, Struhsaker 1971). This maternal inexperience is also associated with primiparity, but there is no way to test any potential significance, as there were no known primiparous females in the sample. The prediction may also not have been supported, because young mothers in the sample pool may have had allomothering experience, gaining practice in maternal care by babysitting younger siblings or other juveniles in the group (Fairbanks 1990, Fairbanks 2002, Johnson et al. 1980).

My final prediction, that the !Gariep females would have higher average HCC than the Soetdoring females due to greater anthropogenic stressors, was not supported. Primate populations have been found to have higher stress levels in environments with greater levels of anthropogenic impact, including increased human contact, habitat degradation, and climate change (Busch & Hayward 2009, Carlitz et al. 2016, Crespi et al. 2013, Dettmer et al. 2014, Fourie et al. 2015). Additionally, !Gariep Dam's greater levels of anthropogenic interference present riskier foraging options than in Soetdoring, which may increase stress levels. Though the foraging may be riskier, it is also higher-reward, being more plentiful and providing higher caloric value. Access to good nutrition has been linked to earlier sexual maturation and, therefore, potential onset of parity (Cheney et al. 1988, Loudon et al. 2014, Novak et al. 2013, Schmitt et al. 2020). There may not have been a correlation between HCC and site because a higher degree of nutritional stress experienced by the females of Soetdoring due to their lack of access to the higher quality foods that are available in !Gariep may have offset the discrepancy between their stress levels and those of the females in !Gariep. HCC was found to have a significant relationship with population site when both male and female vervets were included in the data. The fact that population and HCC were only correlated when the entirety of the sampled individuals were included, but not when only one sex was included may indicate that the sample size was too small without both sexes.

Further evidence for the sample size being too small without incorporating most or all of the sampled animals is that no models with a single predictor for HCC produced significant correlation. Subset selection could not produce a model with an adjusted r^2 larger than 0.3 until at least four predictors were incorporated into the model. The five predictor (dental age, body mass, parity status, lactation status, and population site) model was able to incorporate all sampled animals and was the best predictor out of the 64 possible models. The five predictor model was the simplest available model that could best predict the HCC of the sampled animal. When putting into the formula an individual’s dental age, body mass, parity status, lactation status, and population site, it could predict a HCC closer to the animal's actual HCC than any of the other 63 models, save the full six-predictor model. The five predictor model had the same predictive power as the full model using all six predictor variables, because parity status inherently incorporates sex. It was also simpler, not needing the sixth predictor variable, sex. The fact that all predictors were needed to form a decently predictive model indicates small sample size, particularly given the lack of significant interaction effects indicating that no specific variables together are responsible for that predictive power.

Problems and Limitations

The relatively small sample size was the result of the Covid-19 pandemic travel restrictions and lab backups that caused the focus of my thesis to change multiple times. As a result, the statistical analyses lacked power. This inherently limits the certainty with which conclusions can be drawn. However, not every formula tested provided insignificant results. Notably, body mass and parity were found to have a strong relationship, consistent with most predictions based in a life history framework. This connection illustrates that the small sample size, while limiting, is not prohibitive.

Additionally, the limitations of the sample include that there were no primiparous females to compare to the nulliparous and multiparous females. Nulliparous, primiparous, and multiparous individuals may have different relationships with the other available variables, so the scope of this research was limited by one-third of the possible parity statuses being absent from the sample pool. Only nulliparity and multiparity were analyzed in my research.

Implications and Future Directions

Parity status and cortisol have been found to be positively correlated in some nonhuman primate populations in a number of studies (Dettmer et al. 2015, Petrullo et al. 2019). Other studies have reported higher cortisol levels in nulliparous primates (Kalin et al. 1998). Still other studies have found no significant relationship between parity and cortisol (Gonzalez et al. 2009, Sullivan et al. 2011). Most of these studies did not have hypotheses directly relating parity and cortisol, so the reasons some populations exhibit various relationships between parity and cortisol concentration is not clear. Further, many studies that do mention parity and cortisol focus on contrasting primiparity and multiparity, rather than nulliparity and parity, limiting their ability to be directly compared with the results of this study.

I hypothesized that in the populations of !Gariep and Soetdoring, a female vervet monkey's parity status and HCC would be significantly correlated, with multiparous females having higher HCC than nulliparous females. With respect to this hypothesis, I made four predictions related to female maternity and socioecology. The hypothesis was not supported. This may mean that no such correlation exists, or it may be indicative that the sample size and statistical power were insufficient to find an existing correlation. Socioecological variables, particularly population site, provide more significant results than life history variables such as parity. Body mass's significant correlation with parity and population site is noteworthy. The difference in body mass between the nulliparous and multiparous females of !Gariep and Soetdoring indicate that the two sites affected the body masses of the females.

Further study should also be considered with the goal of examining these relationships with a larger, or different, sample pool. This research could be expanded upon by including more populations of South African vervet monkeys in the data, providing greater sample numbers, statistical power, and possibly the inclusion of primiparous females. It is also possible that in the intervening 12 years between the samples taken and the analysis for this research that the demographics of the populations have changed, and that this research could be expanded on.

Ideally, future studies of these populations should procure a bigger sample size and potentially more variables. Social rank is has been found to impact primates' stress levels, and even relate to ecological factors in some populations (Abbott et al. 2003, Qin et al 2013, Whitten 1983). Rank is one variable I did not have access to for the sampled individuals that could be used in other, similar studies. Future research should use multiple linear regression to look at relationships between cortisol levels, life history stages such as parity status, and socioecological variables including social rank, anthropogenic interference, and population. The interplay between the variables of parity and population in this research show a potential relationship with food or nutrition that would be worth exploring in further studies. Anthropogenic changes to foraging behaviors and diet may affect nutrition and health in ways that affect female life history, influencing or being influenced by parity status.

Overall, the model using five of the predictor variables (dental age, body mass, parity status, lactation status, and population site) came nearest to approximating the values of HCC in the study animals. It was equal to the full six predictor model that included sex, because parity status included sex – no females were listed as "N/A;" all males were listed as "N/A." The lack of distinction seen here is indicative of the sample size being too small to identify any one variable as critical to the HCC value. It is the combination of the variables that makes the formula function as a predictive model. Therefore, including more sampled animals and more variables would work to the make the model stronger.

CHAPTER 8: CONCLUSION

My research thesis tested the hypothesis that a South African vervet female's parity status has an effect on her levels of chronic stress levels. This was done by analyzing the HCC of adult female vervet monkeys of two different categories of parity from two different sites for statistically significant correlation between HCC and parity status. Though this research failed to reject the null hypothesis and was unable to establish a correlation between parity status and HCC, it proposed new questions regarding anthropogenic influence on a population's stress levels. Life history stages, socioecological factors, and stress levels all interact with one another in ways that may potentially be further explored in the future. Parity and stress, if related in these populations, may vary due to the various levels of anthropogenic stressors present. Stress levels and their effects on health, reproductive and maternal behavior, and life history outcomes can play a crucial role in our understanding of these animals and deserve to be explored all possible populations.

REFERENCES

Abbott D.H., Keverne E.B., Bercovitch F.B., Shivley C.A., Mendoza S.P., Saltzman W., Snowden C.T., Ziegler T.E., Banjevic M., Garland Jr. T., & Sapolsky R.M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior* 43:67-82.

Beehner J.C. & Bergman T.J. (2017). The next step for stress research in primates: To identify relationships between glucocorticoid secretion and fitness. *Hormones and Behavior* 91:68-83.

Bolter D.R. (2011). A Comparative Study of Growth Patterns in Crested Langurs and vervet Monkeys. *Anatomy Research International* 2011. doi: 10.1155/2011/948671

Brommer J.E. (2000). The evolution of fitness in life-history. *Biological Reviews* 75(3): 377-404.

Busch D.S. & Hayward L.S. (2009). Stress in a conservation context: A discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biological Conservation* 142: 2844-2853.

Butynski T.M. (2002). The Guenons: An Overview of Diversity and Taxonomy. In *The Guenons: Diversity and Adaptation in African Monkeys*, ed. Glenn M.E. & Cords M. New York: Kluwer Academic Publishers. p 3-13.

Carlitz E.H.D., Kirschbaum C., Stalder T., & van Schaik C.P. (2014). Hair as a long-term retrospective cortisol calendar in orang-utans (*Pongo spp.*): New perspectives for stress monitoring in captive management and conservation. *General and Comparative Endocrinology* 195: 151-156.

Carlitz E.H.D., Miller R., Kirschbaum C., Gao W., Hänni D.C., & van Schaumburg C.P. (2016). Measuring Hair Cortisol Concentrations to Assess the Effect of Anthropogenic Impacts on Wild Chimpanzees (Pan troglodytes). PLOSOne 11(4):e0151870.

Carrera S.C., Sen S., Heistermann M., Lu A., & Beehner J.C. (2020). Low rank and primiparity increase fecal glucocorticoid metabolites across gestation in wild geladas. *General and Comparative Endocrinology* 293.

Cheney D.L. (1981). Intergroup encounters among free-ranging vervet monkeys. *Folia Primatologica* 35: 124-146.

Cheney D.L. & Seyfarth R.M. (1981). Selective Forces Affecting the Predator Alarm Calls of Vervet Monkeys. *Behaviour* 76(1-2): 25-61.

Cheney D.L. & Seyfarth R.M. (1983). Nonrandom dispersal in Free-Ranging Vervet Monkeys: Social and Genetic Consequences. *The American Naturalist* 122(3): 392-412.

Cheney D.L., Seyfarth R.M., Andelman S.J., & Lee P.C. (1988). Reproductive success in vervet monkeys. In *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*, ed. Clutton-Brock T.H. Chicago: University of Chicago Press.

Clutton-Brock T. & Janson C. (2012). Primate socioecology at the crossroads: Past, present, and future. *Evolutionary Anthropology* 21(4): 136-150.

Cramer J.D., Gaetano T., Gray J.P., Grobler P., Lorenz J.G., Freimer N.B., Schmitt C.A., & Turner T.R. (2013). Variation in Scrotal Color Among Widely Distributed Vervet Monkey Populations (*Chlorocebus aethiops pygerythru*s and *Chlorocebus aethiops sabaeus*). *American Journal of Primatology* 75(7):752-762.

Crespi E.J., Williams T.D., Jessop T.S., & Delehanty B. (2013). Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? *Functional Ecology* 27: 93-106.

Davenport M.D., Tiefenbacher S., Lutz C.K., Novak M.A., & Meyer J.S. (2006). Analysis of endogenous cortisol concentrations in the hair of rhesus macaques. *General and Comparative Endocrinology* 147:255-261.

Dettmer A.M., Murphy A.M., Guitarra D., Slonecker E., Suomi S.J., Rosenberg K.L., Novak M.A., Meyer J.S., & Hinde K. (2018). Cortisol in Neonatal Mother's Milk Predicts Later Infant Social and Cognitive Functioning in Rhesus Monkeys. *Child Development* 89(2):525-538.

Dettmer A.M., Novak M.A., Meyer J.S., & Suomi S.J. (2014). Population density-dependent hair cortisol concentrations in rhesus monkeys (*Macaca mulatta*). *Psychoneuroendocrinology* 42:59-67.

Dettmer A.M., Novak M.A., Suomi S.J., & Meyer J.S. (2012). Physiological and Behavioral Adaptation to Relocation Stress in Differentially Reared Rhesus Monkeys: Hair Cortisol as a Biomarker for Anxiety-related Responses. *Psychoneuroendocrinology* 37(2):191-199.

Dettmer A.M., Novak M.F.S.X., Meyer J.S., & Suomi S.J. (2009). Hair Cortisol Predicts Object Permanence Performance in Infant Rhesus Macaques (*Macaca mulatta*). *Developmental Psychobiology* 51(8):706-713.

Dettmer A.M., Rosenberg K.L., Suomi S.J., Meyer J.S., & Novak M.A. (2015). Associations between Parity, Hair Hormone Profiles during Pregnancy and Lactation, and Infant Development in Rhesus Monkeys (*Macaca mulatta*). *PLOSOne* 10(7): e0131692.

Ellis B.J., Figueredo A.J., Brumbach B.H., & Schlomer G.L. (2009). Fundamental Dimensions of Environmental Risk. *Human Nature* 20: 204-268.

Estrada A., Garber P.A. Rylands A.B., Roos C., Fernandez-Duque E., Di Fiore A., Nekaris K.A., Nijman V., Heymann E.W., Lambert J.E., Rovero F., Barelli C., Setchell J.M., Gillespie T.R., Mittermeier R.A., Arregoitia L.V., de Guinea M., Gouveia S., Dobrovolski R., Shanee S., Shanee N., Boyle S.A., Fuentes A., MacKinnon K.C., Amato K.R., Meyer A.L.S., Wich S., Sussman R.W., Pan R., Kone I., & Li B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances* 3:e1600946.

Fairbanks L.A. (1988). Mother-infant behavior in vervet monkeys. *Behavioral Ecology and Sociobiology* 23:157-165.

Fairbanks L.A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour* 40(3): 553-562.

Fairbanks L.A. (2002). Juvenile Vervet Monkeys: Establishing Relationships and Practicing Skills for the Future. In *Juvenile Primates*, ed. Pereira M.E. & Fairbanks L.A. New York: Oxford University Press.

Fairbanks L.A. & McGuire M.T. (1985). Relationships of vervet mothers with sons and daughters from one through three years of age. *Animal Behaviour* 33: 40-50.

Fairbanks L.A. & McGuire M.T. (1987). Mother-infant relationships in Vervet Monkeys: Response to new adult males. *International Journal of Primatology* 8: 351-366.

Fairbanks L.A. & McGuire M.T. (1995). Maternal condition and the quality of maternal care in vervet monkeys. *Behaviour* 132: 733–754.

Fourie N.H., Turner T.R., Brown J.L., Pampush J.D., Lorenz J.G., & Bernstein R.M. (2015). Variation in vervet (*Chlorocebus aethiops*) hair cortisol concentrations reflects ecological disturbance by humans. *Primates* 56:365-373.

Garber P.A., McKenney A., Bartling-John E., Bicca-Marques J.C., De la Fuente M.F., Abreu F., Schiel N., Souto A., & Phillips K.A. (2020). Life in a harsh environment: the effects of age, sex, reproductive condition, and season on hair cortisol concentration in a wild non-human primate. *PeerJ* 8:e9365.

Gomiendo M. (1989). Differences in fertility and suckling patterns between primiparous and multiparous rhesus mothers (*Macaca mulatta*). *Journals of Reproduction & Fertility* 87:529-542.

Gonzalez A., Jenkins J.M., Steiner M., & Fleming A.S. (2009). The relation between early life adversity, cortisol awakening response and diurnal salivary cortisol levels in postpartum women. *Psychoneuroendocrinology* 34:76-86.

Grant K.S., Worlein J.M., Meyer J.S., Novak M.A., Kroeker R., Rosenberg K., Kenney C., & Burbacher T.M. (2016). A longitudinal study of hair cortisol concentrations in *Macaca nemestrina* mothers & infants. *American Journal of Primatology* 79(2):1-9.

Grobler J.P. & Turner T.R. (2010). A novel trap design for the capture and sedation of vervet monkeys (*Chlorocebus aethiops*). *South African Journal of Wildlife Research* 40(2): 163-168.

Grubb P.J., Butynski T.M., Oates J.F., Bearder S.K., Disotell T.R., Groves C.P., & Struhsaker T.T. (2003). Assessment of the diversity of African primates. *International Journal of Primatology* 24:1301-1357.

Hauser M.D. (1994). The Transition to Foraging Independence in Free-Ranging Vervet Monkeys. In *Behavioral Aspects of Feeding*, ed. Galef Jr. B.G., Mainardi M., & Valsecchi P. Langhorne, PA: Hardwood Academic Publishers.

Heimbürge S., Kanitz E., & Otten W. (2019). The use of hair cortisol for the assessment of stress in animals. *General and Comparative Endocrinology* 270:10-17.

Hill K. (1993). Life history theory and evolutionary anthropology. *Evolutionary Anthropology* 2: 78-88.

Hinde K., Skibiel A.L., Foster A.B., Del Rosso L., Mendoza S.P., & Capitano J.P. (2015). Cortisol in mother's milk across lactation reflects maternal life history and predicts infant temperament. *Behavioral Ecology* 26(1):269-281.

Horrocks J.A. & Hunte W. (2002). Interactions Between Juveniles and Adult Males in Vervets: Implications for Adult Male Turnover. In *Juvenile Primates*, ed. Pereira M.E. & Fairbanks L.A. New York: Oxford University Press.

Isbell L.A. (1995). Seasonal and social correlates of changes in hair, skin, and scrotal condition in vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *American Journal of Primatology* 36:61-70.

Isbell L.A. (1998). The Vervets' Year of Doom. In *The Primate Anthology*, ed. Ciochon R.L. & Nisbett R.A. Upper Saddle River, New Jersey: Prentice Hall.

Isbell L.A., Cheney D.L., & Seyfarth R.M. (1990). Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behavioral Ecology and Sociobiology* 27: 351-358.

IUCN. (2022). *Chlorocebus pygerythrus*. The IUCN Red List of Threatened Species 2022.

Janson C.H. (2000). Primate Socio-Ecology: The End of a Golden Age. *Evolutionary Anthropology* 9(2): 73-86.

Jarrett J.D., Bonnell T., Jorgensen M.J., Schmitt C.A., Young C., Dostie M., Barrett L., & Henzi S.P. (2020). Modeling variation in the growth of wild and captive juvenile vervet monkeys in relation to diet and resource availability. *American Journal of Physical Anthropology* 171(1): 89-99.

Jasinska A.J., Schmitt C.A., Service S.K., Cantor R.M., Dewar K., Jentsch J.D., Kaplan J.R., Turner T.R., Warren W.C., Weinstock G.M., Woods R.P., & Freimer N.B. (2013). Systems Biology of the Vervet Monkey. *ILAR Journal* 54(2):122-143.

Johnson C., Koerner C., Estrin M., & Duoos D. (1980). Alloparental care and kinship in captive social groups of vervet monkeys (*Cercopithecus aethiops sabaeus*). *Primates* 21: 406-415.

Kalin N.H., Shelton S.E., Rickman M., Davidson R.J. (1998). Individual Differences in Freezing and Cortisol in Infant and Mother Rhesus Monkeys. *Behavioral Neuroscience* 112(1):251-254.

Kappeler P.M., Pereira M.E., & Van Schaik C.P. (2003). Primate Life Histories and Socioecology. In *Primate Life Histories and Socioecology*, ed. Kappeler P.M. & Pereira M.E. Chicago: University of Chicago Press.

Kapoor A., Lubach G., Hedman C., Ziegler T.E., & Coe C.L. (2014). Hormones in infant rhesus monkeys’ (*Macaca mulatta*) hair at birth provide a window into the fetal environment. *Pediatric Research* 75:476-481.

Laudenslager M.L., Jorgensen M.J., & Fairbanks L.A. (2012). Developmental patterns of hair cortisol in male and female nonhuman primates: Lower hair cortisol levels in vervet males emerge at puberty. *Psychoneuroendocrinology* 37(10):1736-1739.

Lee P.C. (1984). Ecological Constraints On the Social Development of Vervet Monkeys. *Behaviour* 91(4): 244-261.

Lee P.C. (1987). Nutrition, fertility, and maternal investment in primates. *Journal of Zoology* 213(3): 409-422.

Loudon J.E., Grobler J.P., Sponheimer M., Moyer K., Lorenz J.G., & Turner T.R. (2014). Using the Stable Carbon and Nitrogen Isotope Compositions of Vervet Monkeys (*Chlorocebus pygerythrus*) to Examine Questions in Ethnoprimatology. *PLOSOne* doi: https://doi.org/10.1371/journal.pone.0100758.

Maestripieri D. (2011). Emotions, Stress, and Maternal Motivation in Primates. *American Journal of Primatology* 73: 516-529.

Mitchell G. & Stevens C.W. (1968). Primiparous and multiparous monkey mothers in a mildly stressful social situation: First three months. *Developmental Psychobiology* 1(4):280-286.

Novak M.A., Hamel A.F., Kelly B.J., Dettmer A.M., & Meyer J.S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behavioural Science* 143(2-4):135-149.

Petrullo L., Hinde K., & Lu A. (2019). Milk hormones predict early infant growth. *American Journal of Human Biology* doi: 10.1002/ajhb. 23315.

Pusey A.E. & Packer C. (1987). Dispersal and Philopatry. In *Primate Societies* ed. Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W., & Struhsaker T.T. Chicago: The University of Chicago Press. p 250-266.

Qin D.D., Rizak J.D., Feng X.L., Chu X.X., Yang S.C., Li C.L., LV L.B., Ma Y.Y., & Hu X.T. (2013). Social rank and cortisol among female rhesus macaques (*Macaca mulatta*). *Zoological Research* 34(E2):E42-E49.

R Core Team. (2022). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rakotoniaina J.H., Kappeler P.M., Kaesler E., Hämäläinen A.M., Kirschbaum C., & Kraus C. (2017). Hair cortisol concentrations correlate negatively with survival in a wild population. *BMC Ecology* 17:30.

Rodríguez R.L., Danzy Cramer J., Schmitt C.A., Gaetano T.J., Grobler J.P., Freimer N.B., & Turner T.R. (2015). The static allometry of sexual and nonsexual traits in vervet monkeys. *Biological Journal of the Linnaean Society* 114(3):527-537.

Ross C. & Jones K.E. (1999). Socioecology and the evolution of primate reproduction rates. In *Comparative Primate Socioecology*, ed. Lee P.C. New York: Cambridge University Press. 73-110.

Rowell T.E. (1970). Reproductive cycles of two Cercopithecus monkeys. *Reproduction* 22(2):321-338.

Saltzman W. & Abbott D.H. (2009). Effects of Elevated Circulating Cortisol Concentrations on Maternal Behavior in Common Marmoset Monkeys (*Callithrix jacchus*). *Psychoneuroendocrinology* 34(8):1222-1234.

Saltzman W. & Maestripieri D. (2011). The Neuroendocrinology of Primate Maternal Behavior. *Progress in Neuro-Psychopharmacology and Biological Psychiatry* 35(5):1192-1204.

Sapolsky R.M. (2021). Glucocorticoids, the evolution of the stress-response, and the primate predicament. *Neurobiology of Stress* 14:100320.

Schmitt C.A., Rich A.M., Parke S.R., Blaszczyk M.B., Cramer J.D., Freimer N.B., Grobler J.P., & Turner T.R. (2020). Anthropogenic food enhancement alters the timing of maturational landmarks among wild savanna monkeys (*Chlorocebus pygerythrus*). bioRxiv doi: https://doi.org/10.1101/2020.04.18.048314.

Schultner J., Kitaysky A.S., Gabrielsen G.W., Hatch S.A., & Bech C. (2013). Differential reproductive responses to stress reveal the role of life-history strategies within a species. *Proceedings of the Royal Society B* 280(1771).

Schwegel M.A., Filazzola A., Chapman C.A., & Schoof V.A.M. (2022). Breeding Seasonality in Female Vervet Monkeys (*Chlorocebus pygerythrus*) Living in an Anthropogenic Landscape. *International Journal of Primatology* doi: 10.1007/s10764-022-00313-y

Setchell J.M., Fairet E., Shutt K., Waters S., & Bell S. (2017). Biosocial Conservation: Integrating Biological and Ethnographic Methods to Study Human-Primate Interactions. *International Journal of Primatology* 38: 401-426.

Sharpley C.F., Kauter K.G., & McFarlane J.R. (2010). Hair cortisol concentration differs across site and person: localization and consistency of responses to a brief pain stressor. *Physiological Research* 59(6): 979-983.

Skinner J.D. & Chimimba C.T. (2005). The Mammals of the Southern African Subregion (3rd ed.). New York: Cambridge University Press.

Snaith T.V. & Chapman C.A. (2007). Primate Group Size and Interpreting Socioecological Models: Do Folivores Really Play by Different Rules? *Evolutionary Anthropology* 16(3): 94-106.

Struhsaker T.T. (1971). Social Behaviour of Mother and Infant Vervet Monkeys (*Cercopithecus aethiops*). *Animal Behaviour* 19(2):233-234.

Sullivan E.C., Hinde K., Mendoza S.P., & Capitiano J.P. (2011). Cortisol Concentrations in the Milk of Rhesus Monkey Mothers are Associated with Confident Temperament in Sons, but not Daughters. *Developmental Psychobiology* 53(1):96-104.

Terborgh J. & Janson C.H. (1986). The Socioecology of Primate Groups. *Annual Review of Ecology and Systematics* 17: 111-136.

Thierry B. (2008). Primate Socioecology, the Lost Dream of Ecological Determinism. *Evolutionary Anthropology* 17(2): 93-96

Turner T.R., Anapol F., & Jolly C.J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology* 103(1): 19-35.

Turner T.R., Coetzer W.G., Schmitt C.A., Lorenz J.G., Freimer N.B., & Grobler J.P. (2016). Localized population divergence of vervet monkeys (*Chlorocebus spp*.) in South Africa: Evidence from mtDNA. *American Journal of Physical Anthropology* 159(1):17-30.

Turner T.R., Schmitt C.A., & Danzy Cramer J. (2019a). Ethnoprimatology and Savanna Monkeys. In *Savanna Monkeys*, ed. Turner T.R., Schmitt C.A., & Danzy Cramer J. New York: Cambridge University Press. p 235-243.

Turner T.R., Schmitt C.A., & Danzy Cramer J. (2019b). Behavioral Ecology of Savanna Monkeys. In *Savanna Monkeys*, ed. Turner T.R., Schmitt C.A., & Danzy Cramer J. New York: Cambridge University Press. p 109-126.

Turner T.R., Schmitt C.A., & Danzy Cramer J. (2019c). Savanna Monkey Taxonomy. In *Savanna Monkeys*, ed. Turner T.R., Schmitt C.A., & Danzy Cramer J. New York: Cambridge University Press. p 31-54.

Turner T.R., Schmitt C.A., & Danzy Cramer J. (2019d). Life History of Savanna Monkeys. In *Savanna Monkeys*, ed. Turner T.R., Schmitt C.A., & Danzy Cramer J. New York: Cambridge University Press. p 163-198.

Turner T.R., Schmitt C.A., Danzy Cramer J., Lorenz J., Grobler J.P., Jolly C.J., & Freimer N.B. (2018). Morphological variation in the genus *Chlorocebus*: Ecogeographic and anthropogenically mediated variation in body mass, postcranial morphology, and growth. *American Journal of Physical Anthropology* 166(3): 682-707.

Uno H., Tarara R., Else J.G., Suleman M.A., & Sapolsky R.M. (1989). Hippocampus Damage Associated with Prolonged and Fatal Stress in Primates. *The Journal of Neuroscience* 9(5):1705-1711.

van de Waal E., Bshary R., & Whiten A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour* 90: 41-45.

Wallen K. & Zehr J.L. (2004). Hormones and History: The Evolution and Development of Primate Female Sexuality. *Journal of Sex Research* 41(1): 101-112.

Warren W.C., Jasinska A.J., García-Pérez R., Svardal H., Tomlinson C., Rocchi M., Archidiacono N., Capozzi O., Kremitzki M., Graves T., Chiang C., Hughes J., Tran N., Huang Y., Ramensky V., Choi O., Jung Y.J., Schmitt C.A., Juretic N., Wasserscheid J., Turner T.R., Wiseman R.W., Tuscher J.J., Karl J.A., Schmitz J.E., Zahn R., O'Connor D.H., Redmond E., Nisbett A., Jacquelin B., Müller-Trutwin M.C., Brenchley J.M., Dione M., Antonio M., Schroth G.P., Kaplan J.R., Jorgensen M.J., Thomas G.W.C., Hahn M.W., Raney B.J., Aken B., Nag R., Schmitz J., Churakov G., Noll A., Stanton R., Webb D., Thibaud-Nissan F., Nordborg M., Marques-Bonet T., Dewar K., Weinstock G.M., Wilson R.K., & Freimer N.B. (2015). The genome of the vervet (*Chlorocebus aethiops sabaeus*). *Genome Research* 25:1921-1933.

Whitten P.L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology* 5(2): 139-159.

Whitten P. (2019). Socioecology of Vervet Monkeys. In *Savanna Monkeys*, ed. Turner T.R., Schmitt C.A., & Danzy Cramer J. New York: Cambridge University Press. p 127-132.

Whitten P.L. & Turner T.R. (2009). Endocrine mechanisms of primate life history trade-offs: Growth and reproductive maturation in vervet monkeys. *American Journal of Human Biology* 21(6): 754-761.

Wickham H., Chang W., Henry L., Takahashi K., Wilke C., Woo K., Yutani H., &Dunnington D. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Yamanashi Y. (2018). Is Hair Cortisol Useful for Animal Welfare Assessment? Review of Studies in Captive Chimpanzees. *Aquatic Mammals* 44(2):201-210.