Theses and Dissertations   Hunter College

Summer 8-9-2018

Allomaternal Care by Conspecifics Impacts Activity Budgets of Colobus guereza Mothers

Dominique L. Raboin
CUNY Hunter College

[How does access to this work benefit you? Let us know!](#)

Allomaternal Care by Conspecifics Impacts Activity Budgets of *Colobus guereza* Mothers

by

Dominique Raboin

Submitted in partial fulfillment

of the requirements for the degree of

Master of Arts

Animal Behavior and Conservation, Hunter College

City University of New York

2018

July 30, 2018	Andrea Baden
_____	_____
Date	Signature of First Reader
July 30, 2018	Jessica Rothman
_____	_____
Date	Signature of Second Reader

Table of Contents

List of Figures

List of Tables

Acknowledgments

Abstract

In primate societies, caring for infants involves nursing, protection, provisioning, and carrying -

all energetically taxing states for mothers. The cost of holding and carrying clinging infants often

constrains mothers from moving and traveling, potentially reducing their food and energy intake.

Alternatively, when an infant is physically separated from their mother they are at risk of

predation from birds of prey or other large mammals. This requires a high level of vigilance from

mothers, often further deterring them from acquiring the food and energy that they need.

Allomaternal care (AMC) is hypothesized to provide mothers with a way to safely detach from

their infants to feed and forage, allowing them to replenish their depleted energy stores. This

thesis aimed to test this idea by investigating the function of AMC in a wild, forest-living

colobine (*Colobus guereza*). The objective of this study was to document the nature of AMC in

C. guereza and to determine the potential feeding benefits for lactating mothers during AMC.

Research was conducted in Kibale National Park, Uganda, where seven mother-infant dyads in

three groups of *C. guereza* were observed during six consecutive months (from the beginning of

July through the end of December, 2017) resulting in a total of 661 observation hours (N=864

AMC bouts). The average AMC bout length was 49 seconds (range=638 seconds, SD=0.01).

Juveniles and subadults handled infants more often than adults (Mann-Whitney U, $p<0.01$), and

females handled infants more often than males (Mann-Whitney U, $p<0.01$). An infant's distance

to mother and the infant's nearest neighbor's age and sex best predicted the occurrence of AMC

(Logistic regression, $p<0.001$). Infant age was the best predictor of the duration of AMC bouts

(GLMM, $p<0.05$). Activity budgets significantly differed when lactating mothers were with and

without their infants (Kruskal Wallis, $p<0.01$). Lactating mothers fed more than other activities

when their infants were handled by conspecifics (Z=3.49, df=1, $p<0.01$). Lactating mothers fed

and rested for longer durations during AMC bouts vs. non-AMC bouts (Wilcoxon, $p<0.001$). No differences were found between feeding rate and metabolizable energy consumed during feeding bouts that took place during AMC vs. non-AMC (Wilcoxon $p>0.05$, Wilcoxon $p>0.05$). These results provide evidence that AMC in *C. guereza* gives lactating mothers the opportunity to replenish energy through feeding and resting without clinging infants.

Introduction

Primate infant care involves gestation, lactation, protection, provisioning, and carrying –

all energetically taxing states for mothers (Isler & van Schaik, 2012; König, 1997; Trivers,

1972). Holding and carrying infants constrain mothers from moving and traveling, potentially

reducing their energy intake (Gilchrist, 2007). Alternatively, when an infant is not clinging to

their mother, they are at risk of predation or falling from a tree (Gilchrist, 2007; Onderdonk,

2000). Infant protection requires high levels of vigilance from mothers, which may further deter

them from getting the energy and nutrients that they need. Allomaternal care (AMC), the care of

offspring by conspecifics, is commonly exhibited throughout the primate order and may enable

mothers to safely feed and rest in the absence of their infants (Isler & van Schaik, 2012; Lukas &

Clutton-Brock, 2012). This behavior is exhibited throughout the animal kingdom in insects,

birds, fish, and some mammals including primates, rodents, and large carnivores, with the

purpose of maximizing reproductive output and infant survival (Cockburn, 1998b; Isler & van

Schaik, 2012; Lee et al., 2016; Lukas & Clutton-Brock, 2012; Schubert et al., 2009; Young et al.,

2006).

There are many different types of AMC behaviors including babysitting, protection,

provisioning, carrying, and allomaternal nursing (Isler & van Schaik, 2012; Mitani & Watts,

1997). There are different benefits and costs to all parties involved (mother, infant, helper) for

each of these specific behaviors. Generally, benefits of AMC to mothers include increased time

for feeding, foraging, and resting (Isler & van Schaik, 2012; Lukas & Clutton-Brock, 2012;

Mitani & Watts, 1997); benefits of AMC to infants include opportunities to learn social skills

and strengthen their immune system via individuals other than their mother (Rapaport & Brown,

2008); and benefits of AMC to helpers include opportunities to learn parenting skills and trade

helping behaviors for other benefits, such as increased grooming or rank (Muroyama, 1994;

Tiddi et al., 2010). The costs of AMC to mothers and infants are somewhat aligned, as they

include risk of infant mistreatment, risk of infant fall, and risk of infant death (Gilchrist, 2007;

McKenna, 1979). For helpers, time spent investing in conspecific's infants is time lost for

feeding, foraging, resting, and investing in their own reproductive fitness. Thus, costs of AMC to

helpers include potential loss of energy and nutrient deficiency (Gilchrist, 2007; Mitani & Watts,

1997).

Primate Allomaternal Care Review

Allomaternal care (AMC), the care of offspring by non-parental figures, is seen

throughout the animal kingdom. Insects, birds, fish, and mammals use this method of infant care

to maximize their reproductive output and infant survival, although the specific benefits to

mothers, infants, and helpers differ from species to species (Cockburn, 1998a; König, 1997;

Lukas & Clutton-Brock, 2012; Mitani & Watts, 1997; Riedman, 1982; Schubert, Pillay, &

Schradin, 2009; Trivers, 1972). Species within the primate order use AMC at varying

frequencies and intensities. The first aim of this thesis is to discuss the variation of AMC

throughout the primate order by considering types of care, the breeding systems of several

primate families and subfamilies associated with AMC, the evolutionary theories behind AMC,

and by couching AMC within the broader animal literature. The second aim of this thesis is to

conduct an in-depth study of a wild, forest-living colobine (*Colobus guereza*) to further

investigate the function of AMC in this species by collecting and analyzing data on maternal

feeding frequencies during AMC. In total, this thesis should provide the reader with a thorough

background of primate AMC and a comprehensive examination of the purpose of AMC in one specific primate species.

Types of Care

AMC refers to infant care provided by group members other than the infant's mother (Lukas & Clutton-Brock, 2012). This helping behavior has been observed in fathers (e.g., siamangs, *Symphalangus syndactylus*, (Lappan, 2008)); siblings (e.g., marmosets, *Callithrix kuhlii* (Ginther & Snowdon, 2009)); and in unrelated group members (ringtail lemur, *Lemur catta* (Pereira & Izard, 1989)). Although paternal care is not common in mammals, we would expect biological fathers to help rear their own infants more than we would expect unrelated individuals to help with infant care (Buchan, Alberts, Silk, & Altmann, 2003). The investment in the survival of offspring by fathers is classified as AMC, however it is also simply parental care. AMC provided by siblings is also to be expected, as siblings share half of their genes. AMC provided by unrelated individuals is far more perplexing and costly than infant care provided by biological relatives.

Babysitting.

Primate infant care and AMC behaviors can be categorized into five behavioral categories: babysitting, protection, provisioning, carrying, and allomaternal nursing (see Table 1) (Isler & van Schaik, 2012). Each of these behaviors encompasses a range of actions directed toward or performed for the benefit of a conspecific's infant and vary in their degree of cost to the helper, mother, and infant. Babysitting, although vague and encompassing a variety of events, is one of the least costly AMC behaviors. It is also the most common form of AMC observed in primates, and is found in lemurs, lorises, platyrrhines, catarrhines, and apes (Huck & Fernandez-Duque, 2013; Riedman, 1982). Vigilance, restraining, playing, touching, grooming,

inspecting, nuzzling, huddling, and comforting are all attributes of babysitting (Bădescu, Sicotte, Ting, & Wikberg, 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007). Babysitting gives lactating mothers the opportunity to groom, feed, and forage without a clinging infant or the need for constant vigilance (Isler & van Schaik, 2012). It does not have to be energetically taxing to the helpers, but the cost of babysitting is lost time for feeding and investing in one's own reproductive output. Costs exist to mothers and infants as well, as babysitters are not always as careful with infant well being as mothers may be.

Protection

If a behavior is directed toward the mother, but is still beneficial to the infant (e.g., maternal protection), it can be considered AMC due to the advantage the infant receives (Gilchrist, 2007). Protection is when group members shield or protect another individual and/or individuals from some threat or hazard, such as by using warning vocalizations or physically challenging the source of some threat or hazard. Although not necessarily enacted for the sake of infants, group protection benefits infants of any group by preventing attack from intra or inter-specific threats. Infants are not only at high risk of mortality from interspecific predators, such as aerial attacks by eagles or terrestrial attacks by large cats, but also from intraspecific takeovers and infanticide (Buchan et al., 2003; Hrdy, 1974; Isler & van Schaik, 2012; Ross & Regan, 2000). Sometimes protection is beneficial at the group level and not just for infants, yet there is also evidence of infant protection of intra- and extra- group infanticidal males (Hrdy, 1974). Protection can be physically and energetically taxing to helpers since it can potentially involve fighting and/or injury.

Provisioning

Provisioning involves any activity that has a direct energetic benefit to the recipient, such as allowing infants to share food (Isler & van Schaik, 2012; König, 1997). Provisioning can be directed toward the infant or mother, either while the mother is pregnant or lactating (Isler & van Schaik, 2012). Provisioning is only common in callitrichines and humans, although also occasionally seen in lemurs and bi-parental breeders such as owl monkeys (*Aotus sp.*) and gibbons (*Hylobates sp.*) (Huck & Fernandez-Duque, 2013; Isler & van Schaik, 2012; Meehan, Quinlan, & Malcom, 2013; Mitani & Watts, 1997). Provisioning of human mothers and weaned offspring has been used to partially explain increased brain size and longer life expectancy in humans (Isler & van Schaik, 2012). Although provisioning is only common in some primate species, it can be energetically costly to helpers due to potential hunger and/or nutrient deficiency.

Carrying

Carrying is an energetically costly form of AMC that involves an individual using their arms, legs, or tail to hold, carry, or transport an infant in a physically supportive way (Bădescu et al., 2015), and varies in cost across species due to the variability in infant/adult weight ratios. It is a common type of AMC observed in lemurs, most playtrrhines, most catarrhines, and apes (Isler & van Schaik, 2012; Mitani & Watts, 1997; Murray, Stanton, Lonsdorf, Wroblewski, & Pusey, 2016; Tecot, Baden, Romine, & Kamilar, 2013) Carrying behavior can be performed by males, females, adults, and juveniles depending on the species (Isler & van Schaik, 2012). Carrying by helpers can occur with or without the mother and infant's permission, and in some species, can lead to infant mistreatment (Hrdy, 1974).

Allomaternal nursing

Allomaterning nursing, or non-offspring nursing, occurs when a lactating female nurses an infant other than her own. Although uncommon, allomaternal nursing is found in several different primate taxa, including some lemurs, some callitrchines, some catarrhines and other mammalian taxa across the animal kingdom (Isler & van Schaik, 2012; Mitani & Watts, 1997; Packer, Lewis, & Pusey, 1992; Tecot et al., 2013). Allomaternal nursing is more common in species with larger litters, but also occurs in species with single-offspring as well (Packer et al., 1992). In species with single-offspring, allomaternal nursing often occurs as function of milk-theft or after a helper's infant has died (Packer et al., 1992). Allomaternal nursing can be helpful to the infant and costly to the helper due to the energy-loss associated with lactation, or can be helpful to communally breeding mothers and infants at the group level (Gittleman & Thompson, 1988). Both of these scenarios are seen in the primate order.

Table 1. *Types of Care and Cost to Actors*

Type of Care	Cost to Helper	Cost to Mother	Cost to Infant
Babysitting	Time lost for feeding, foraging, grooming	Risk of infant mistreatment	Risk of mistreatment; risk of disease transmission
Protection	Potential physical harm or injury	Risk of infant mistreatment	Risk of mistreatment; risk of misplaced aggression
Provisioning	Time lost for feeding, foraging, grooming; loss of energy; risk of hunger and nutrient deficiency	Risk of infant mistreatment	Risk of mistreatment; risk of disease transmission

Type of Care	Cost to Helper	Cost to Mother	Cost to Infant
Carrying	Time lost for feeding, foraging, grooming; loss of energy	Risk of infant mistreatment; risk of dropping infant; risk of infant traveling too far away	Risk of mistreatment; risk of falling; risk of traveling too far from mother; risk of disease transmission
Allomaternal Nursing	Time lost for feeding, foraging, grooming; loss of energy; risk of hunger and nutrient deficiency	Risk of infant mistreatment	Risk of mistreatment; risk of disease transmission

Breeding Systems

The occurrence of AMC and the types of AMC used by each species is associated with its breeding system, or the social mechanism by which males and females of each species are able to reproduce offspring (Lukas & Clutton-Brock, 2012). Breeding systems are characterized by reproductive skew, infant rearing, and whether or not helping behavior is observed. Specific breeding systems are usually associated with specific group characteristics of species, such as group size, group composition, and dispersal patterns. I examined the reproductive skew, dispersal patterns, and helping behaviors of over 100 different primate species with the aim of classifying each species' breeding system (Erb & Porter, 2017; Isler & van Schaik, 2012; Mitani & Watts, 1997; Tecot et al., 2013). Table 1 summarizes the six different breeding systems established.

Table 2. *Primate Breeding Systems*

Bi-parental care: A breeding system characterized by low to high reproductive skew.

Helping behavior is present and obligatory from the putative father.

Plural breeding: A breeding system characterized by low to medium reproductive skew.

Helping behavior is not observed.

Singular breeding: A breeding system characterized by low to high reproductive skew.

Solitary females rear infants alone and no helping behavior is observed.

Plural breeding with AMC: A breeding system characterized by low to high reproductive

skew. Helping behavior is present and facultative.

Communal breeding: A breeding system characterized by low to medium reproductive skew.

Helping behavior is present and facultative. Infants are communally crèched or denned.

Cooperative breeding: A breeding system characterized by high reproductive skew. Helping

behavior is present and obligatory.

AMC in the Animal Kingdom

As noted above, AMC is observed in insects, birds, fish, and mammals other than

primates, such as rodents and large carnivores (Cockburn, 1998b; Isler & van Schaik, 2012; Lee,

Heim, & Meyer, 2016; Lukas & Clutton-Brock, 2012; Schubert et al., 2009; Young et al., 2006).

Studying AMC in other taxa assists in the research of the evolution and maintenance of AMC in primates by revealing patterns and variation in AMC between primates and other animals. The breeding systems of non-primate animals that exhibit AMC vary from plural breeders who use AMC (e.g., cichlid fish, *Cichlidae perissodus* (Lee et al., 2016)), communal breeders (e.g., four-striped mice, *Muridae rhabdomys* (Schubert et al., 2009), and cooperative breeders (e.g., crows, magpies, and jays, *Corvidae sp.* (Ekman & Ericson, 2006). Evidence has shown that the occurrence of monogamy and high levels of kinship within groups are important indicators for the evolution of AMC in birds, insects, and non-primate mammals, although exceptions exist in each category (Lukas & Clutton-Brock, 2012). Reciprocity between helpers and mothers, as well as the direct benefits helpers receive from exhibiting helping behavior, have been shown as key mechanisms to the maintenance of AMC in insects, birds, fish, and mammals who use AMC (Clutton-Brock, 2002).

AMC in Primates

Compared to other animals, primates are unique in that some form of helping behavior is observed in nearly every primate species (Isler & van Schaik, 2012). Meanwhile, helping behavior is only observed in less than half of the species in other groups (Isler & van Schaik, 2012). About 20% of primate species exhibit only protection, 40% exhibit all forms of help without provisioning, and 30% exhibit all forms of help including provisioning (Isler & van Schaik, 2012). The occurrence of AMC, the types of AMC behaviors that are used, and the breeding systems associated with AMC vary between and within differing primate taxa. This section outlines the variability of AMC within the primate order by examining AMC within certain primate taxa.

Strepsirrhines.

Lemurs, lorises, galagos, and pottos make up the suborder strepsirrhini. Most lemurs are either communal or plural breeders who use AMC (Erb & Porter, 2017; Tecot et al., 2013). The exceptions are some of the species in the family Indriidae and three of the species in the genus *Eulemur*, are plural breeders without AMC (Tecot et al., 2013). The slender lorises and galagos are plural breeders who use AMC, but the slow lorises and the potto are generally singular breeders (Isler & van Schaik, 2012; Nekaris, 2006). There are more communal breeders among the strepsirrhines than any other primate taxa, which most notably include *Varecia variegata*, *Varecia rubra*, *Microcebus murinus*, and *Cheirogaleus medius*. Carrying and babysitting are the two most common types of AMC exhibited by strepsirrhines, with only some species exhibiting allomaternal nursing and provisioning (Isler & van Schaik, 2012; Tecot et al., 2013).

Platyrrhines.

Breeding systems vary among the five families of the New World monkeys, though not nearly as much variation as within the strepsirrhines. The family Cebidae, which includes capuchins and squirrel monkeys, are plural breeders who use AMC (Baldovino & Di Bitetti, 2008; Biben, 1992; Fragaszy, Baer, & Adam-Curtis, 1991; Isler & van Schaik, 2012; Manson, 1999; Mitani & Watts, 1997; O'Brien & Robinson, 2013; Tiddi, Aureli, & Schino, 2010). Typical helping behaviors include carrying, provisioning, playing, and nursing. Carrying is the most commonly exhibited helping behavior within this family. In the family Cebidae, potential helpers and the infants who receive AMC vary in age, rank, and relatedness (O'Brien & Robinson, 2013). Wedged-capped capuchin (*Cebus olivaceus*) helpers are typically juveniles or young adults, of equal rank to the infant's ranking, and siblings or kin (O'Brien & Robinson, 2013). Meanwhile, tufted capuchin infants (*Cebus nigritus*) receive allomaternal nursing from

adult and juvenile females, almost always of a lower rank than the infant's mother's rank, with the same frequency from related and unrelated individuals (Baldovino & Di Bitetti, 2008).

The breeding system of the family Aotidae is classified as bi-parental breeders (Fernandez-Duque, Juarez, & Di Fiore, 2008; Huck & Fernandez-Duque, 2012; Isler & van Schaik, 2012; Mitani & Watts, 1997; Rotundo, Fernandez-Duque, & Dixson, 2005). Although plenty of helping behavior is observed in this family, AMC is most often performed by the putative father. Owl monkey groups are generally made up of one male, one female, an infant, and older subadult or juvenile offspring (Huck & Fernandez-Duque, 2013). The male who is present at the time of conception is the genetic father, but if the genetic father is replaced by another male before or after the birth of an infant, the subsequent male will provide care for the infant at similar rates as the genetic father would (Huck & Fernandez-Duque, 2012). Carrying, babysitting and provisioning are common types of helping behaviors within this family. Callitrichines are cooperative breeders across the subfamily, exhibiting obligate helping behavior and high reproductive skew (Bales, Dietz, Baker, Miller, & Tardif, 2000; Caperos, Sánchez, Peláez, Fidalgo, & Morcillo, 2011; Díaz-Muñoz, 2016; Fite et al., 2005; Ginther & Snowdon, 2009; Isler & van Schaik, 2012; Mitani & Watts, 1997; Saito, Izumi, & Nakamura, 2011). Carrying and provisioning are helping behaviors that are necessary for infant survival, and are mostly performed by subadult and adult males and females (Fite et al., 2005; Ginther & Snowdon, 2009; Isler & van Schaik, 2012). Notably, the breeding female in most callitrichine species uses reproductive suppression to keep other females from breeding, ensuring that there are enough available helpers to assist with offspring rearing (Erb & Porter, 2017).

Pitheciidae varies in breeding systems within the family. The genera Callicebus, Pithecia, and Chiropotes are plural breeders who use AMC (Cox, Tappan, & Engelhardt, 1987; Isler &

van Schaik, 2012; Mitani & Watts, 1997). Carrying and babysitting are common helping behaviors within this family (Isler & van Schaik, 2012). The genus *Cacajao* differs from the rest, however, with the majority of infant care performed by the father (Fragaszy et al., 1991). Thus, the genus *Cacajao* is classified as bi-parental breeders. The family Atelidae, largest of the New World monkeys, often vary in breeding system within species. However, nearly every species in the family does exhibit AMC to some degree. Thus, the Atelids are plural breeders who use AMC (Calegaro-Marques & Bicca-Marques, 1993; Clarke, Glander, & Zucker, 1998; Evans, Pavelka, Hartwell, & Notman, 2012; Isler & van Schaik, 2012; Mitani & Watts, 1997; Slater, Schaffner, & Aureli, 2007). Carrying and babysitting are the most common helping behaviors observed within this family, and allomaternal nursing is observed in some species within this taxa (Calegaro-Marques & Bicca-Marques, 1993; Clarke et al., 1998; Evans et al., 2012; Slater et al., 2007).

Cercopithecines.

The cercopithecines, which includes baboons, macaques, guenons, and vervet monkeys, vary between plural breeders with and without AMC (Buchan et al., 2003; Chism, 2000; Fruteau, van de Waal, van Damme, & Noë, 2011; Huchard et al., 2010; Isler & van Schaik, 2012; Maestripieri, 1994a; Mitani & Watts, 1997; Silk, 1999). Following the principle that even a small frequency of helping behavior should still be classified as AMC, I conclude that all of the baboons, macaques, and vervet monkeys are plural breeders with AMC (Buchan et al., 2003; Chism, 2000; Fruteau et al., 2011; Hrdy, 1974; Huchard et al., 2010; Maestripieri, 1994a, 1994b; Silk, 1999). The patas monkey is also a plural breeder who uses AMC (Muroyama, 1994). Carrying and babysitting are the most common helping behaviors observed within this family, and allomaternal nursing is observed more often in this family than any other primate family

(Isler & van Schaik, 2012; Li, Ren, Li, Zhu, & Li, 2013; Packer et al., 1992) Only the guenons

do not exhibit helping behavior, which makes them plural breeders (Isler & van Schaik, 2012;

Mitani & Watts, 1997).

Colobines.

The colobines are overwhelmingly plural breeders who use AMC (McKenna, 1979).

Helping behavior is facultative in this family, commonly exhibited as carrying and babysitting,

although allomaternal nursing occurs as well (Bădescu et al., 2015; Borries, Launhardt, Epplen,

Epplen, & Winkler, 1999; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007; Dunham & Opere,

2016; Hrdy, 1974; Li et al., 2013; Pan et al., 2014; Ross & Regan, 2000; Stanford, 1992; Sutton,

Hoskins, & Arnould, 2015; Xiang, Sayers, & Grueter, 2009; Yao et al., 2012; Zhao, Tan, & Pan,

2008). Helpers are generally female and helping behavior is observed as early as the first day of

life (Bădescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007; McKenna, 1979). It has

been suggested that AMC is so ubiquitous among colobines due to their egalitarian social

structure, facilitated by low intragroup dominance hiearchies (McKenna, 1979; Snaith &

Chapman, 2007). One of the notable exceptions is the Sumatran surili (*Presbytis melalophos*)

who is a plural breeder, as helping behavior has not been observed in this species (Isler & van

Schaik, 2012).

Non-human apes.

The non-human apes are made up of the chimpanzees, bonobos, gorillas, orangutans,

gibbons, and siamangs. Gibbons and siamangs live in socially monogamous groups, leading to a

bi-parental breeding system (Isler & van Schaik, 2012; Lappan, 2008, 2009; Mitani & Watts,

1997). Carrying, babysitting, and provisioning are provided by the putative fathers, and less

frequently, by older siblings (Isler & van Schaik, 2012; Lappan, 2008; Mitani & Watts, 1997).

Chimpanzees, bonobos, and gorillas are all plural breeders who use AMC (Bădescu, Watts, Katzenberg, & Sellen, 2016; Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999; Meier, Hemelruk, & Martin, 2000; Murray et al., 2016). Chimpanzees and bonobos carry, provision, and babysit conspecific's infants, while gorillas only carry and babysit (Isler & van Schaik, 2012; Mitani & Watts, 1997). Orangutans are singular breeders, with the mothers rearing their infants alone (Beaudrot, Kahlenberg, & Marshall, 2009; Isler & van Schaik, 2012; Mitani & Watts, 1997).

Evolution of AMC

AMC in primates requires the capacity for cooperation and as such is seen in species with relatively complex sociality (Isler & van Schaik, 2012). Whether pro-sociality and increased cognitive performance must already be present to develop AMC, or vice versa, is still a debated topic in evolutionary anthropology (J. M. Burkart & van Schaik, 2016; Lukas & Clutton-Brock, 2012; Silk, 2007). The socio-cognitive tasks required to perform AMC can be useful in other aspects of life, such as the ability to monitor group members and interpret their signals (Judith Maria Burkart & van Schaik, 2009). Yet the causal link between advanced socio-cognitive abilities and AMC, in either direction, is still missing (Judith Maria Burkart & van Schaik, 2009). Sociality evolves when it is more beneficial than costly to associate with individuals outside of direct kin (Silk, 2007). Although caring for a conspecific's offspring may seem too costly of a behavior to lead to sociality, the inclusive fitness model allows for limited altruism and a constraint on competitive behavior (Hamilton, 1964). Depending on the species, the benefits some helpers receive from participating in AMC include increased breeding opportunities, practice for mothering, and increased favor from dominant group members (Lehmann & Keller, 2006). In addition, AMC may improve group cohesion, benefiting the

mother, helper, and infant (Muroyama, 1994). The benefits mothers, infants, and helpers receive

from using AMC help us to trace the evolutionary history of this infant care behavior

(Bergmüller, Johnstone, Russell, & Bshary, 2007).

Evolutionary Theories

As AMC is not only observed in primates, but also insects, birds, fish, and other

mammals as well, evolutionary theories for the occurrence and maintenance of AMC are

discussed from an animal-wide perspective (see Table 3).

Kin Selection Hypothesis.

Hamilton's rule, that altruistic behavior will be selected for if the benefits to the recipient

multiplied by the coefficient of relatedness outweigh the cost to the actor, is the foundation of

kin selection (Hamilton, 1964). This rule implies that kin will engage in costly behaviors in order

to benefit the outcome of their shared genes. The costliness of the behavior increases as the

coefficient of relatedness increases, ensuring that costly altruism occurs between closely related

individuals. For many species, kin selection acts as a form of "family insurance," allowing kin to

care for each other's offspring and adopt each other's offspring in the event of a mother's death

(Eberle & Kappeler, 2006).

Hamilton's rule is seen at work in a number of species that fit the kin selection model. In

an obligate cooperatively breeding bird (*Pomatostomus rufceps*), 98% of group members with

kin present choose to help and 100% of helpers direct their care towards related offspring

(Browning, Patrick, Rollins, Griffith, & Russell, 2012). Macaques, baboons, and vervet monkeys

maintain close bonds with their female matrilineal kin and provide care for each other's offspring

(Silk, 2002). Mouse lemurs (*Microcebus murinus*) forms day-nests with close matrilineal kin and

babysit, groom, and nurse each other's offspring (Eberle & Kappeler, 2006). In a study of 44

species, within-group relatedness and AMC were positively correlated in mammals (Briga, Pen,

& Wright, 2012). Despite all of the evidence for the evolution of AMC through kin selection, in

many species helpers provide care to unrelated offspring and mothers (Clutton-Brock, 2002).

Biological Market Hypothesis.

The biological market hypothesis aims to explain what the kin selection hypothesis can't

- why unrelated individuals engage in AMC. The hypothesis is based off of the theory of

reciprocal altruism, which means benefits are exchanged reciprocally especially between

unrelated individuals (Trivers, 1972). This reciprocal exchange of benefits is observed in

cooperatively breeding cichlid fish (*Neolamprologus pulcher*) (Balshine-Earn, Neat, Reid, &

Taborsky, 1998; Bergmuller, Heg, & Taborsky, 2005). The cichlid fish helpers gain direct fitness

benefits for helping with infant care by gaining protection from the group and having the

possibility of inheriting dominant breeding positions (Balshine-Earn et al., 1998). If the helpers

abandon the brood and attempt to return, other group members punish the runaways by attacking

or evicting. Alternatively, a tufted capuchin (*Cebus apella nigritus*) female's chance of gaining

access to an infant for handling is highly increased if they groom the mother of the infant (Tiddi

et al., 2010). Similarly, female patas monkeys (*Erythrocebus patas*) exchange grooming for

AMC (Muroyama, 1994). Helpers will groom mothers in order to gain access to infants, and

mothers will groom helpers in exchange for babysitting and carrying infants. Grooming is more

frequent between unrelated individuals than between kin. This reciprocal exchange of benefits

improves group cohesion and strengthens the likelihood that infants will be cared for in the event

of a mother's death.

Group Augmentation Hypothesis.

An alternative to kin selection is the group augmentation hypothesis, which states that individuals help conspecific's with infant care in exchange for membership in a large group, where individuals are more likely to survive longer (Kokko, Johnstone, & Clutton-Brock, 2001). Group augmentation is supported by delayed reciprocity, where new group members help with the care of unrelated offspring in order to benefit from group size. Some species of birds, such as acorn woodpeckers (*Melanerpes formicivorus*), favor group-living despite vacant breeding sites due to the benefits of food hoarding (Kokko et al., 2001). A cooperatively breeding bee (*Exoneura bicolor*) has been shown to prefer group nesting even when dispersal opportunities are available due to lower survival rates of offspring in nests with smaller group sizes (Bull & Schwarz, 1997). This trend is seen in several other taxa, including mammals (*Scuriata scuriatta*) and other insects (*Solenopsis wagneri*) (Clutton-Brock, 2002). Nonetheless, group augmentation is rarely identified as the sole driving force for AMC due to the variation in the degree of help provided based on relatedness between the helpers and the recipients (Browning et al., 2012; Cockburn, 1998a). There is little to no support for this hypothesis in primates.

Ecological Constraints Hypothesis.

The ecological constraints hypothesis aims to explain delayed dispersal in species of birds, fish and primates (e.g., callitrichines) who use AMC by demonstrating that delayed dispersal is necessary to maintain the presence of helpers (Bergmuller et al., 2005; Hatchwell & Komdeur, 2000). If there aren't any vacant breeding sites outside of the natal group or if variation in climate decreases available food sources, individuals may choose to delay dispersal and remain in their natal group, helping to rear conspecific's offspring until their own potential opportunity to breed (Cockburn & Russell, 2011). It has been proposed that *Campylorhynchus* wrens remain at the natal nest as helpers due to the lack of available breeding opportunities upon

dispersal (Rabenold, 1990). Similarly, the cooperatively breeding fish, *Neolamprologus pulcher,* reduce helping behavior and disperse when breeding opportunities outside of the group are available, and remain in the group as helpers when outside breeding opportunities are not available (Hatchwell & Komdeur, 2000). Delayed dispersal and helping behaviors are observed in callitrichines, however it is unclear if this is due to ecological constraints (Díaz-Muñoz, 2016). However, the ecological constraints hypothesis falls short due to an inability to explain why AMC occurs in some species, but not in others.

Life History Hypothesis.

The life history hypothesis claims that some species have certain life history traits that predispose them to evolve AMC (Hatchwell & Komdeur, 2000). Some of these traits include long juvenile and adolescent periods, low dispersal rates, and altricial infants at birth (Isler & van Schaik, 2012). This hypothesis is applied to socioecological traits as well, where species with egalitarian dominance relations should be more willing to share the burden of infant care due to less intraspecific competition. In certain colobine species such as *Colobus guereza*, feeding adaptations lead to less intragroup competition for resources, which fosters a safe environment for mothers to trust conspecifics with infant care (McKenna, 1979). However, many species, such as *Macaca sylvanus,* do not fit well into the life history model with a despotic relationship between females, but still exhibit AMC (Paul, 1999).

Learning to Mother Hypothesis.

The learning to mother hypothesis states that nulliparous individuals help conspecifics with infant care in order to learn how to parent their own potential offspring (Lancaster, 1971; McKenna, 1979). This hypothesis has been examined in vervet monkeys (*Cercopithecus aethiops*), where juvenile females frequently carry, groom, and huddle conspecific's infants

(Lancaster, 1971). Nulliparous female *Colobus vellerosus* monkeys were also found to handle

infants more often than parous females in the same group, suggesting that infant handling is

more beneficial for nulliparous females than parous due to a learning component (Bădescu et al.,

2015). There is some support for this theory in other mammals with long juvenile periods, such

as juvenile elephants who allow infants to suckle despite being too young to lactate (Hrdy,

2009). However, delayed juvenility is almost exclusive to primates, which is a necessary

prerequisite for learning to mother as a nulliparous female. This theory fails to account for AMC

by adults, which occurs in high frequency across the primate order.

Infant/Adult Weight Ratio.

In the primate family Callitrichidae, the energetic cost of infant care is the proposed

reason AMC evolved for callitrichines in the first place (Fite et al., 2005). At the time of birth,

callitrichine infants can weigh as much as 15-25% of the mother's body weight, necessitating

help in rearing offspring. Marmoset and tamarin mothers give birth to twins and have short inter-

birth intervals, often conceiving only 2 to 4 weeks after giving birth (Fite et al., 2005).

Callitrichine mothers have evolved to evaluate the degree of help they will receive from their

group and not only plan to conceive accordingly, but also plan to reduce or increase parental

effort accordingly (Bales et al., 2000; Díaz-Muñoz, 2016). Callitrichines are not alone in their

infant/adult weight ratio dilemma. Spectral tarsier infants (*Tarsius spectrum*) are born weighing

20 to 33% of adult weight at birth (Gursky, 2000). Subadult females, and sometimes subadult

males and adult males, must assist with provisioning, carrying, babysitting and protection in

order for infants to survive. These species are unable to care for infants without helpers due to

the infant/adult weight ratio, however this concept clearly only applies to a select few species.

Table 3. *Evolutionary Theories for AMC*

Evolutionary Theory	Description	Example Species	Source
Kin Selection	The cost of helping is worthwhile if kin benefit.	*Microcebus murinus, Pomatostomus rufceps*	Eberle and Kappeler 2006, Browning et al. 2012
Group Augmentation	The cost of helping is worthwhile if group size is large enough.	*Melanerpes formicivorus, Scuriata scuriatta, Exoneura bicolor*	Kokko et al. 2001, Clutton-Brock 2002, Bull and Shwarz 1996
Ecological Constraints	The cost of helping outweighs the lack of resources upon dispersal from natal group.	*Campylorhynchus* wrens, *Neolamprologus pulcher*	Selander 1964, Bergmuller et al. 2005
Life History	The cost of helping is a guaranteed byproduct of certain life history traits.	*Colobus guereza*	McKenna 1979
Learning to Mother	The cost of helping is worthwhile if infant care skills are learned.	*Cevcopithecus aethiops, Colobus vellerosus*	Lancaster 1971, Badescu et al. 2015
Biological Market	The cost of helping is worthwhile if benefits are exchanged reciprocally.	*Erythrocebus patas*, *Neolamprologus*	Muroyama 1994, Balshine-Earne 1998, Tiddi et al. 2010

		pulcher, Cebus apella nigritus	
Infant/Adult Weight Ratio	The cost of helping is a byproduct of necessity.	*Tarsius spectrum, Callithrix kuhlii*	Gursky 2000, Fite et al. 2005

Of these hypotheses, the kin-selection hypothesis and life history hypothesis are most commonly recognized as the drivers for AMC in primates. However, neither theory is able to support the occurrence of AMC throughout the entire primate order. The infant/adult weight ratio hypothesis is well supported for the occurrence of AMC in callitrichines, yet this is also the family that receives the most focus in regards to primate AMC research. Further research is needed to test these theories in other species to better understand the evolutionary importance of helping behavior in primates. It is not known how AMC impacts primate maternal feeding and energy intake. AMC has the potential to alleviate some of the burdens of infant care by allowing mothers to feed and rest without their clinging infants. The following chapter presents research that addresses this hypothesis in a forest-living colobine who uses AMC.

Methods

Hypothesis and Objectives

Even though there are extreme costs to AMC for mothers, infants, and helpers, the infant care strategy still persists throughout nature. There must be some benefits important enough to all parties to allow AMC to continue. We designed a study to examine how the occurrence of AMC affects feeding and energy consumption by *Colobus guereza* mothers to test the hypothesis that AMC in *C. guereza* is beneficial to mothers by allowing for increased maternal feeding time. The goal of this study was to identify any potential feeding benefits to *C. guereza* mothers who

use AMC, whether it be through increased feeding and foraging time and/or increased nutritional intake. To achieve this goal, this study had three main objectives:

1) To describe the form, function, and patterns of AMC in *C. guereza*,

2) To determine maternal activity budgets during AMC bouts,

3) To identify variation in feeding frequency and energy consumption between when mothers are handling infants vs. when infants are handled by mothers.

AMC in *Colobus guereza*

AMC is used by the majority of the colobine monkeys, although AMC in black-and-white colobus monkeys has scarcely been studied when compared to AMC in other colobine species (Bădescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007; Dunbar & Dunbar, 1976; Horwich & Manski, 1975; McKenna, 1979; Oates, 1977; Onderdonk, 2000). This is even more true for wild *Colobus guereza,* with only a few existing papers mentioning the topic of AMC (Dunbar & Dunbar, 1976; Harris, 2004; McKenna, 1979; Oates, 1977). From these few papers, and drawing from similarities in other black-and-white colobus species, it is known that natal attraction and infant handling by conspecifics is facultative, and thus not necessary for survival (Bădescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007; McKenna, 1979; Oates, 1977). The literature implies that AMC occurs most frequently when infants are 0 – 14 weeks (Oates 1977; McKenna 1979; Brent et al. 2008; Badescu et al. 2015). Most mothers are tolerant of infant handling attempts, although infant-directed aggression and infant mistreatment are not uncommon (Oates 1977; McKenna 1979; Harris 2004).

There has yet to be any research investigating the effects of AMC on feeding and foraging strategies of *C. guereza* mothers. *Colobus guerezas* in Kibale National Park (KNP) in Western Uganda, the location of this research, predominantly feed on young leaves, occasionally

also feeding on fruit (Harris & Chapman, 2007; Oates, 1994, 1977). Due to food-processing and food-acquiring adaptations, such as having a multi-chambered foregut to aid in plant matter digestion, *C. guerezas* have reduced intragroup dominance hierarchies, diminishing the need for social competition among females (Davies, 1994; McKenna, 1979; Snaith & Chapman, 2007). However, *C. guereza* are selective feeders and resources vary in quality, nutrition, and availability (Snaith & Chapman, 2007). There is between and within-group competition for food, thus lactating mothers may lose access to feeding and foraging opportunities due to the constraints of infant care.

Colobus guereza are a folivorous African colobine species found throughout eastern Africa. Variation in group size, group composition, and diet exists between differing groups of *C. guereza,* making it difficult to apply generalizations to the species (Dunbar & Dunbar, 1976; Harris, 2004; Harris & Chapman, 2007; Oates, 1977). In KNP, *C. guereza* group size ranges from 4 to 15 individuals, with group core areas ranging from 0.6 to 1.6 ha (Harris & Chapman, 2007; Oates, 1977). Although single-male/multi-female group compositions are common, multi-male/multi-female group compositions are also observed (Dunbar & Dunbar, 1976; Harris & Chapman, 2007; Oates, 1977). Most within-group interactions are non-agonistic (Dunbar & Dunbar, 1976; Oates, 1977). Infants are born throughout the year and infant handling by conspecifics has been observed as early as the first week of life (Harris, 2004; Oates, 1977). *Colobus guereza* infants are born with a white natal coat color and tend to develop their mature coloration by 3 – 4 months of age (Dunbar & Dunbar, 1976; Oates, 1977).

Study Site and Subjects

Data were collected for six months from July until December, 2017 at Makerere University Biological Field Station (MUBFS) at Kanyawara research site in KNP in western

Uganda (0.13-0.41'N and 30.19-30.32'E). KNP is a tropical evergreen forest at medium altitude,

located east of the Ruwenzori Mountains (Chapman, Wrangham, Chapman, Kennard, & Zanne,

1999; Harris & Chapman, 2007). This study followed three groups of *C. guereza* in KNP with

three distinct home ranges. Group sizes ranged between eight and eleven individuals over the

course of the study period, with high variation in group composition (Table 4). Seven mother-

infant dyads were studied between the three groups. Mothers and infants were individually

recognizable due to distinguishing characteristics, ensuring consistency and reliability during

data collection. Infant ages were estimated based on first observations and natal coat color.

Individuals were considered to be infants from 0-1 year old, juveniles from 1-2 years old,

subadults from 2-4 years old, and adults from 4-6 years old until death (Bădescu et al., 2015;

Oates, 1977).

Table 4. *Group Composition of Kasembo, Bingi, and Tail study groups.*

Group	*Total Group	Adult Male	Adult Female	Subadult Male	Subadult Female	Juvenile Male	Juvenile Female	Infant
Kasembo	10	4	2	1	0	0	1	**2
Bingi	11	1	4	2	0	0	1	4
Tail	9	1	5	0	0	0	1	1

*As group composition fluctuated over the study period, the numbers above represent the final composition of each group at the end of data collection (December, 2017). **One infant in Kasembo group disappeared four months into the study period (November, 2017).

Behavioral Observations

Two trained research assistants and I collected data through behavioral observations from

either 7:00-16:00, or 10:00-19:00, depending on the day of the week. Only one group was

followed per week, switching between groups after five days of data collection for a total of 661 hours (28,296 data points) of behavioral data collection. If a group could not be found or we were impeded in collecting data for that group (e.g. elephants in the vicinity), one of the other three study groups was located and followed for the remainder of the day. Data collection was biased towards Kasembo group due to the ease of locating them within their home range. Data were collected using five-minute focal animal follows of mother-infant dyads (Altmann, 1974). Two mother-infant dyads were followed per day, switching between focal dyads every five minutes. Focal dyads were randomized to ensure equal representation during data collection of all mother-infant dyads. One researcher collected on the mother, while the second researcher was responsible for collecting simultaneous infant data. The identity of the observer was always noted and randomized for mother or infant data collection to ensure inter-observer reliability. The sample size is uneven because some infants were present for the entire study period, while others were born later or disappeared before the end of the study period. In addition, group scans were taken using scan sampling every 30 minutes on the hour and half-hour mark to measure group activity and group spread (Altmann, 1974).

The group name, date, recording time, and weather were noted during all data collection. The distance between mothers and infants, mothers and their nearest neighbor, and infants and their nearest neighbor were also recorded. During maternal feeding bouts, plant species and plant part consumed, in addition to the number of leaves/flowers/fruit/seeds consumed, were recorded. During infant handling bouts, the identity of the conspecific ("helper"), their behavior, the infant's behavior, and the mother's reaction were all recorded. Polyspecific associations, all instances of aggression within and between groups, and all vocalizations within and between groups were also noted.

The ethogram was developed to identify relevant activities performed by the focal monkeys (see Table 5). We established that "infant handling" occurred when individuals inspected, groomed, touched, or attempted to touch infants (Bǎdescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007). "Infant carrying" occurred when individuals used their arms or legs to carry or physically support infants for farther than two meters distance (Bǎdescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007). We established that "infant mistreatment" took place when individuals used their arms, legs, or mouth, to distress or harm infants. We established that infants were "playing" when they were with one or more individual engaging in non-agonistic wrestling or biting, or engaging in non-direction jumping or running. The term "huddling" was used to describe one or more individual resting in full body contact with infants. We also referred to "big travel" as any form of locomotion outside of feeding or foraging that spans the distance of three tree lengths.

Table 5. *Ethogram of behaviors recorded in this study*

Term	Definition
Infant Handling	Individuals inspect, groom, touch, or attempt to touch infants
Infant Carrying	Individuals use their arms or legs to carry or physically support infants for farther than two meters distance
Infant Mistreatment	Individuals use their arms, legs, or mouth, to distress or harm infants
Huddling	One or more individual resting in full body contact with infants

Playing	One or more individual engages in non-agonistic wrestling or biting, or engages in non-direction jumping or running

Data Analyses

AMC descriptive analyses.

To describe the form, function, and patterns of AMC in *C. guereza*, the identities of the helpers and the conditions under which AMC took place were explored by generating descriptive statistics. Due to one of the three groups only including one infant, all behavioral durations that were over five-minutes (the duration of the focal observations) were capped at five-minutes (300 seconds) in order to compare durational data between groups. I calculated mean percent time each age-sex class handled infants overall, within and between the three groups. I then used nonparametric Mann-Whitney U tests to identify variation in the age and sex of the helpers. I explored adult helpers (adult males, adult females) vs. non-adult helpers (juvenile females, subadult males). I combined juvenile and subadult helpers into one category due to the potential sex-bias of the three groups only including juvenile females and subadult males. I then explored male helpers vs. female helpers. The age and sex Mann-Whitney U tests were each run twice; once using occurrence data and once using durational data. These tests were run on proportional data between groups due to the oversampling of one group (Kasembo). Kasembo group was sampled more often due to their proximity on the edge of the forest and because this group was the least visited group by elephants.

I then used a logistical regression and a generalized linear mixed model (GLMM) to determine the significance of infant age, nearest neighbor age/sex, distance to mother, and

weather on the occurrence of AMC and the duration of AMC bouts respectively, while

controlling for group and focal infant, using the package lme4 in R Studio (R Core team, 2015).

Infant age ranged from 1 month – 10 months, representing the ages of the seven focal infants

over the course of the study period. The age/sex classes of the nearest neighbors included adult

males (AM), adult females (AF), adult females with a clinging infant (AF/INF) juvenile females

(JF), and subadult males (SAM). These IDs represent the demographics of the available helpers

within the three groups. The distance from infants to their mothers ranged from zero meters to 21

meters. These distances were binned every two meters to reduce the number of factors in these

analyses. Weather included four categories: sunny, rainy, cloudy, sunny/cloudy. Weather

descriptions were classified prior to data collection. The four predictor variables (infant age,

distance to mother, nearest neighbor age and sex, and weather) when calculated for variance

inflation factors (VIF) showed no collinearity and thus were able to be included in the model

(theta=3). I used the dredge function to pick the best model (delta=0.00).

Maternal activity budgets during AMC analyses.

I used a nonparametric Kruskal Wallis test to test for differences in maternal activity

budgets during AMC bouts. I followed this test with a Dunn's post-hoc test. I generated

descriptive statistics to determine maternal activity budgets during all behavioral occurrences,

AMC behavioral occurrences, and non-AMC behavioral occurrences by calculating the

percentage of time engaged in each activity per mother, per day. Feeding, resting, infant care,

traveling, and social activities were taken into consideration when testing for maternal activity

budgets. Feeding included feeding and foraging bouts. An animal was considered at rest when it

was unmoving for ten or more seconds without its clinging infants. Infant care included nursing,

grooming, playing, and resting while physically supporting infants. Traveling included moving

within trees, between trees, and on the ground. Giving and receiving grooming bouts and conspecific-directed vocalizations were classified as social activities.

Maternal feeding/resting patterns and nutritional analyses.

I first generated descriptive statistics to explore the patterns of maternal feeding and resting to gain a clearer picture of maternal energy consumption. To determine the top five plant species consumed by each of the three *C. guereza* groups, I calculated the percentage of each plant species consumed by each group. To explore the importance of feeding and resting to *C. guereza* mothers, I calculated the percentage of all maternal time spent on feeding and resting. I then calculated the percentage of total maternal feeding and resting that took place during AMC bouts.

I used Wilcoxon rank-sum tests to compare the duration of feeding bouts when mothers are handling their infants vs. when conspecifics are handling infants. I also used Wilcoxon rank-sum tests to compare the duration of resting bouts when mothers are handling their infants vs. when conspecifics are handling infants. The purpose of these tests were to compare maternal feeding durations and maternal resting durations during all AMC bouts vs. all non-AMC bouts. To determine if there was a difference between feeding rate during feeding bouts that took place during AMC vs. feeding bouts that took place during non-AMC I first found the feeding rate for each feeding bout by dividing the number of leaves consumed per feeding bout by the duration of the feeding bout (seconds). I used a Wilcoxon rank-sum test to compare these values.

To determine if mothers are consuming more metabolizable energy during feeding bouts that take place during AMC vs. feeding bouts that take place during non-AMC, I used previously collected and analyzed nutritional data (Rothman, 2018), which followed established nutritional laboratory methods (Rothman, Chapman, & van Soest, 2012). I first calculated total

nonstructural carbohydrates (TNC) using the following formula (Conklin-Brittain, Knott, & Wrangham, 2006), where NDF is non-digestible fiber:

$$TNC = 100 – (\%available\ protein + (\%fat – 1) + \%ash + \%NDF)$$

With TNC values I was then able to calculate metabolizable energy (ME) consumed per one-leaf of each of the top five species consumed by each group by using the following formula, adjusted for high-fermentation in colobus diets (Conklin-Brittain et al., 2006; Johnson et al., 2017):

$$ME = (4\ x\ \%TNC) + (4\ x\ \%crude\ protein) + (9\ x\ (\%fat – 1)) + (2.55\ x\ \%NDF)$$

With ME calculated for all maternal feeding bouts for the top 5 species consumed by each group, I calculated the rate of ME per second to make it comparable across feeding bouts of different durations. I then used a Mann-Whitney U test to compare ME during AMC vs. non-AMC within each group and between all groups.

All analyses were completed using R Studio for statistical computing (R Core team, 2015).

Results

AMC descriptive analyses

Over the course of 661 observation hours and 28,296 data points, I observed 864 AMC bouts among the three groups (average=122.8 bouts/individual/group). On average, this equates to 144 AMC bouts per month, 36 AMC bouts per week, and 7.2 AMC bouts per day. The average AMC bout length was 49 seconds (n=864, S.D.=0.01, range=638 seconds). AMC bout lengths ranged from 1 second to over 5 minutes, which means in any given day, AMC bouts could be occurring from anywhere in between 8 seconds to a just under 40 minutes. The most common type of AMC behavior observed among all three groups was "infant handle," which includes individuals inspecting, grooming, touching, or attempting to touch infants (98%). The behaviors "infant carry" (1%) and "play" (1%) were the next most common types of AMC

behaviors. Infant handling occurred consistently for infants aged 1 – 10 months, without much variation based on age.

Non-adult females were the predominant infant handlers in two groups (average=55%), and non-adult males were the predominant infant handlers in the third group (58%). Non-adults (juveniles and subadults) handled infants significantly more often than did adults (U=62622, p<0.01). Likewise, females handled infants more often than did males (U=34232, p<0.01) (see Figure 1). Non-adult individuals handle infants for longer durations than adult individuals (U=34526, p<0.001) (Figure 2). Female individuals handle infants for longer durations than males (U=41166, p<0.001) (Figure 3).
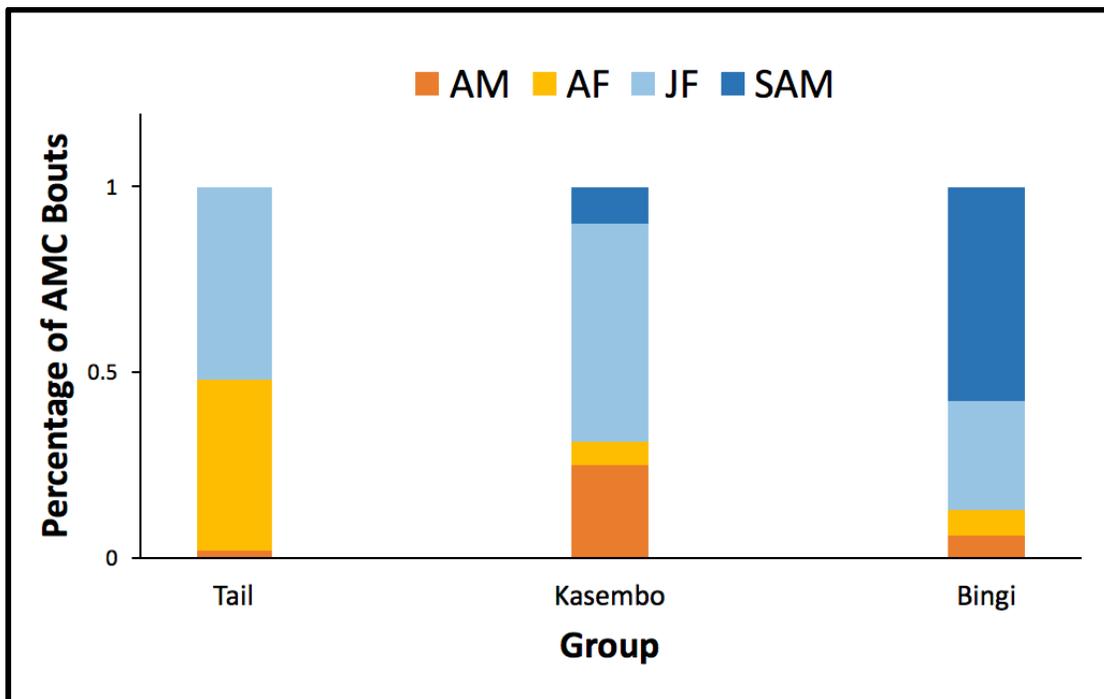

Figure 1. Age and Sex Distribution of Helpers by Group. Group is on the x-axis and proportion of AMC bouts over the study period is on the y-axis. Age and sex of helper is delineated in the stacked bars by color. (AM = adult male, AF = adult female (non-mother), JF = juvenile female, SAM = subadult male).
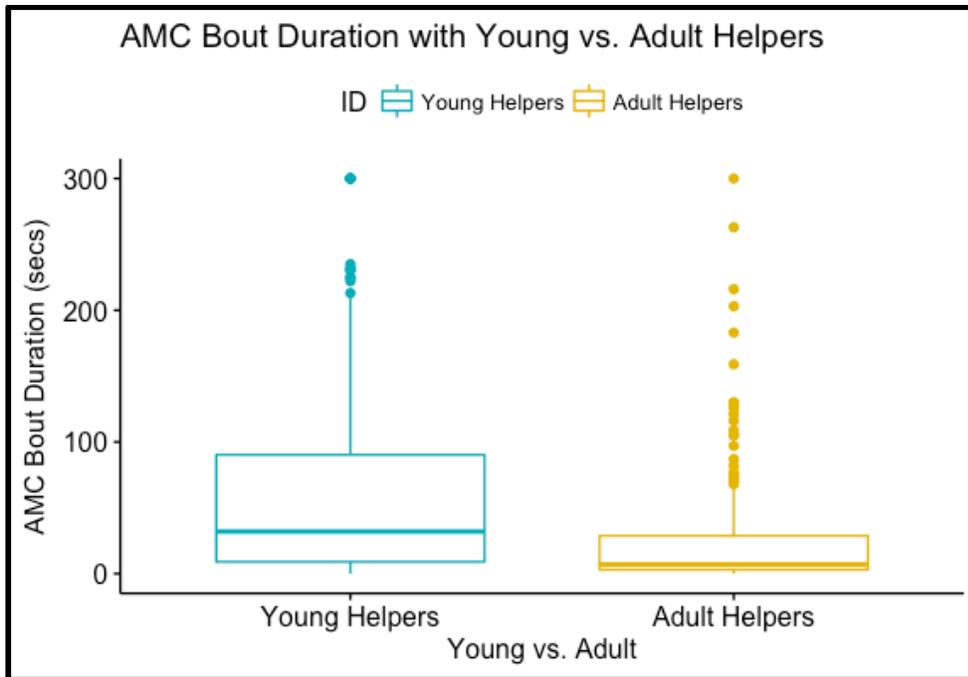
Figure 2. Duration of AMC Bout by Young vs. Adult Helpers. Young vs. adult helper categories are on the x-axis and duration of AMC bout length in seconds is on the y-axis. Young vs. adult helpers are delineated in the boxes by color.
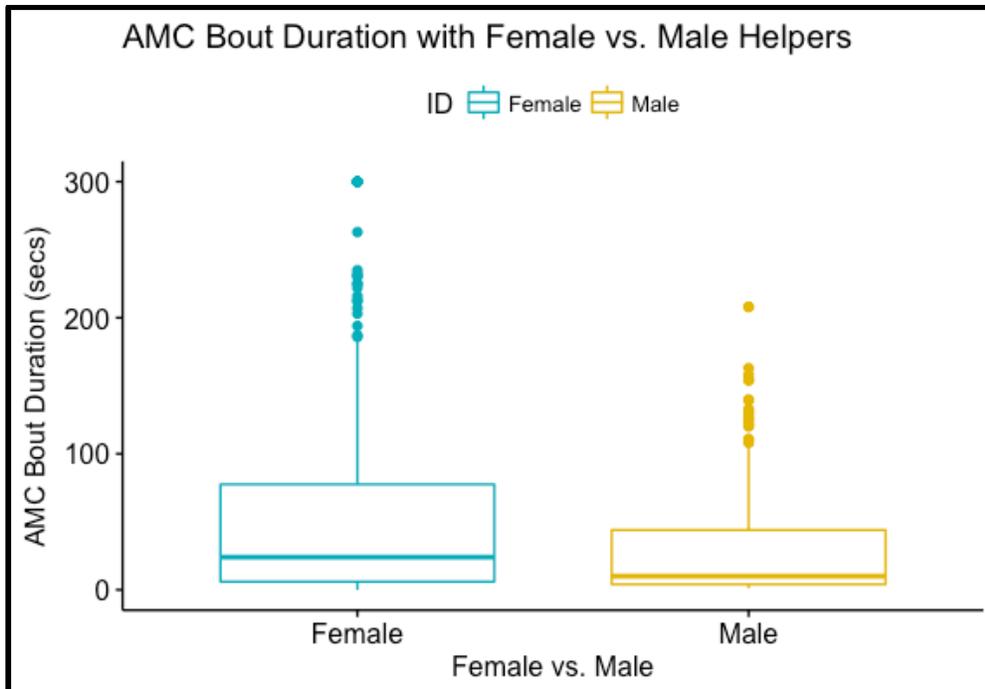
Figure 3. Duration of AMC Bout by Female vs. Male Helpers. Female vs. male helper categories are on the x-axis and duration of AMC bout length in seconds is on the y-axis. Female vs. male helpers are delineated in the boxes by color.

The best model from the logistic regression (that with the lowest AICc score) included distance to mother and nearest neighbor age/sex. Both predictors were significant in the model ($|z|<0.001$). The results of the logistic regression showed juvenile females were the nearest neighbor to infants significantly more often than were adult females (conditional average estimate=3.46, $|z|<0.001$) (Table 6). For every meter increase in nearest neighbor distance, there is a one percent increase in AMC in juvenile females vs. adult females. The results also showed that AMC occurred when infants were 3-5 meters distance from mothers significantly more often than when infants were than 1 meter distance from mothers (conditional average=2.07, $|z|<0.05$). The logistic regression predicted the occurrence of AMC significantly better than the null (X^2 goodness-of-fit test: $p<0.001$). The best model from the GLMM (that with the lowest AICc score) included infant age as a predictor for the duration of AMC bouts. This predictor was

significant in the model (|z|<0.001) (Table 7). The GLMM approached significance in predicting

the duration of AMC bouts better than the null (X^2 goodness-of-fit test: p=0.061).

Table 6. *Conditional average from logistic regression in predicting occurrence of AMC*

Predictors	Estimate	SE	Adjusted SE	Z value	Pr(>|z|)
Distance to Mother	0.00262	0.00029	0.00029	8.942	<2e-16***
Nearest Neighbor	0.00290	0.00035	0.00035	8.103	<2e-16***
Weather	0.00081	0.00060	0.00060	1.344	0.179
Infant Age	0.00015	0.00033	0.00033	0.448	0.654

*** Significant code for 0.001

Table 7. *Conditional average from GLMM in predicting duration of AMC bouts*

Predictors	Estimate	SE	Adjusted SE	Z value	Pr(>|z|)
Infant Age	-7.956	4.021	4.401	1.969	0.049*
Weather	-8.297	5.669	5.700	1.456	0.146
NN	5.756	3.690	3.708	1.552	0.121
Distance to Mother	-3.681	3.503	3.521	1.045	0.296

* Significant code for 0.001

Maternal activity budgets during AMC

Five categories were used to describe maternal activity budgets: feeding, resting, infant care, social, and travel. A difference was detected between the five categories for maternal activity during AMC bouts, and a post-hoc Dunn test showed that mothers are feeding more often than any other activity while their infants are being handled by conspecifics ($p<0.001$; $Z=3.49$, $df=1$, $p<0.01$). During all behavioral occurrences, including during AMC bouts and non-AMC bouts, mothers spend the majority of their time engaged in infant care (52.92%), followed by feeding (23.49%) (SD=42.83) (Figure 4). When mothers are caring for their infants, during non-AMC bouts, mother spend the majority of their time engaged in infant care (55.33%), followed by feeding (21.54%) (SD=40.35) (Figure 5). During AMC bouts, when mothers are without their infants, mothers spend the majority of their time feeding (64.10%), followed by resting (22.49%) (SD=23.82) (Figure 6). AMC bouts made up 4.58% of all behavioral time.
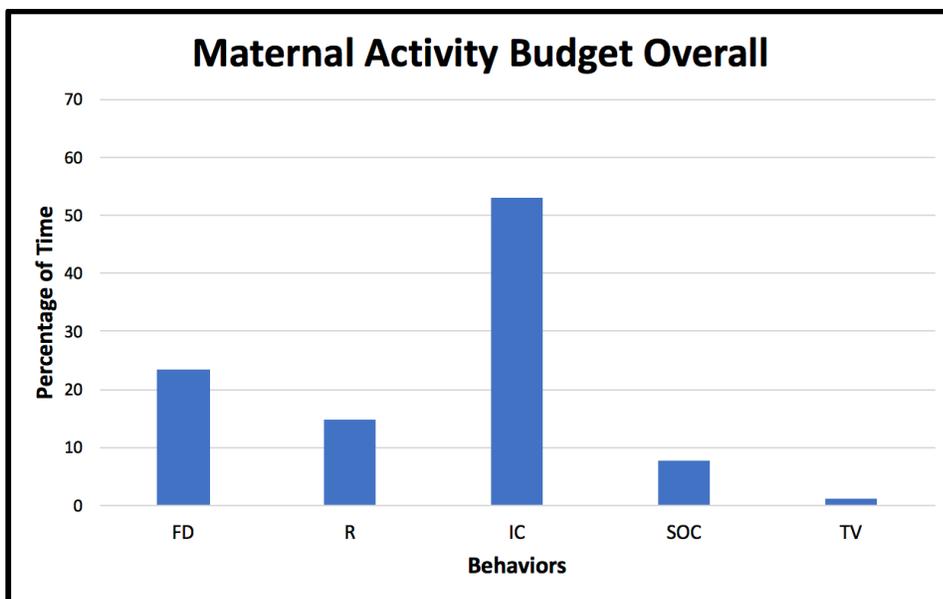

Figure 4. Maternal Activity Budget During All Behavioral Occurrences. Behaviors are listed on the x-axis and percentage of time maternal time is on the y-axis. (FD=Feeding, R=Resting, IC=Infant Care, SOC=Social, TV=Travel).

Figure 5. Maternal Activity Budget During Non-AMC Behavioral Occurrences. Behaviors are listed on the x-axis and percentage of time maternal time is on the y-axis. (FD=Feeding, R=Resting, IC=Infant Care, SOC=Social, TV=Travel).

Figure 6. Maternal Activity Budget During AMC Behavioral Occurrences. Behaviors are listed on the x-axis and percentage of time maternal time is on the y-axis. (FD=Feeding, R=Resting, IC=Infant Care, SOC=Social, TV=Travel).
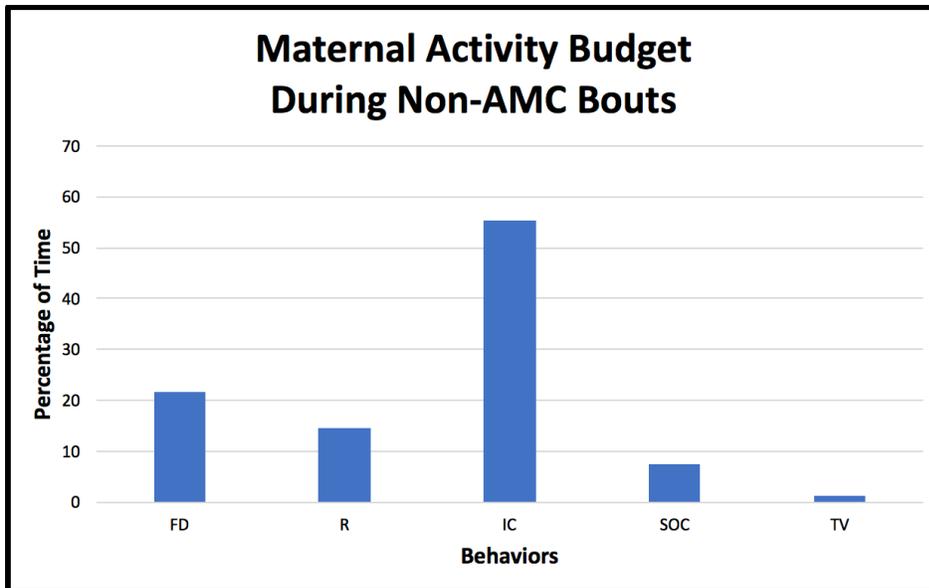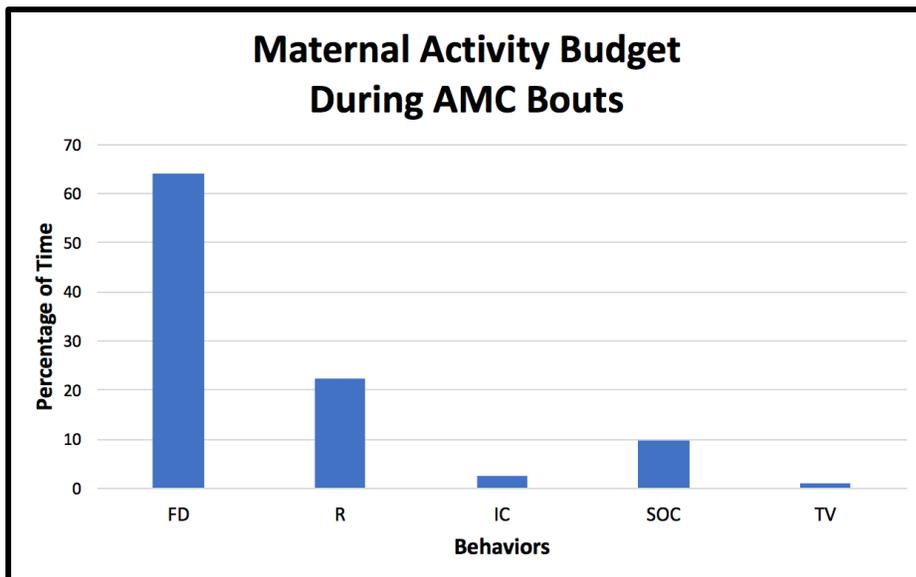
Maternal feeding/resting patterns and nutritional analyses

During all behavioral occurrences, mothers spend 23.49% of their time feeding and 14.77% of their time resting. During non-AMC behavioral occurrences, mothers spend 21.54% of their time feeding and 14.41% of their time resting. During AMC behavioral occurrences, mothers spend 64.10% of their time feeding and 22.49% of their time resting (Table 8). Feeding during AMC bouts made up 12.51% of all feeding time. Mothers fed for longer durations during feeding bouts that took place during AMC vs. feeding bouts that took place during non-AMC (W=2500587.5, p>0.001). Mothers rested for longer durations during resting bouts that took place during AMC vs. resting bouts that took place during non-AMC (W=31526448, p>0.001).

Table 8. *Percentage of maternal feeding and resting time*

	Feeding	Resting
All Time	23.49%	14.77%
Non-AMC Time	21.54%	14.41%
AMC Time	64.10%	22.49%

Figure 7. Feeding Bout Duration During AMC vs. Non-AMC. AMC vs. non-AMC are listed on the x-axis and feeding bout duration in seconds is on the y-axis. AMC vs non-AMC are delineated in the boxes by color.
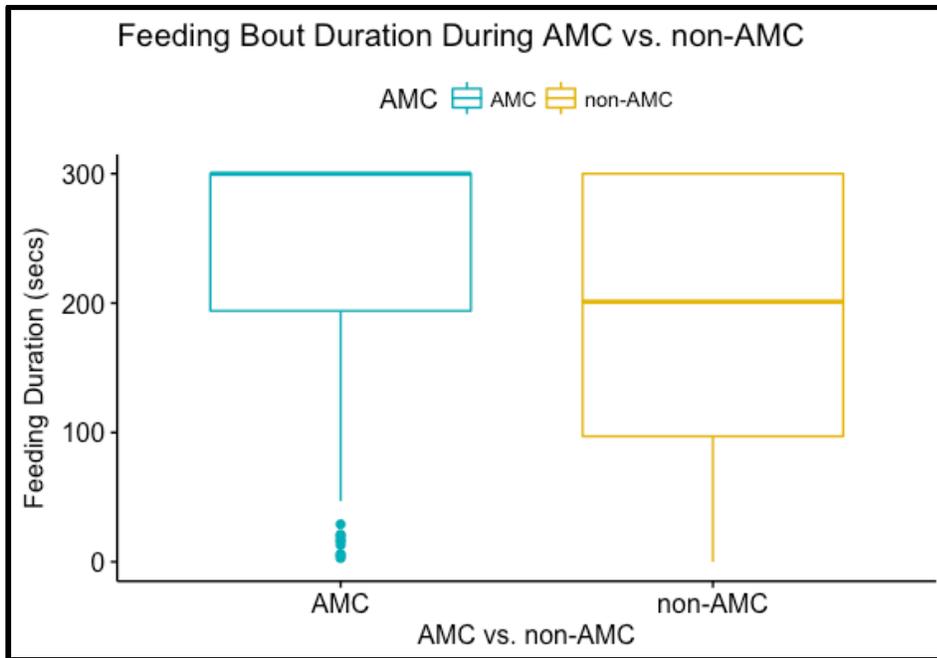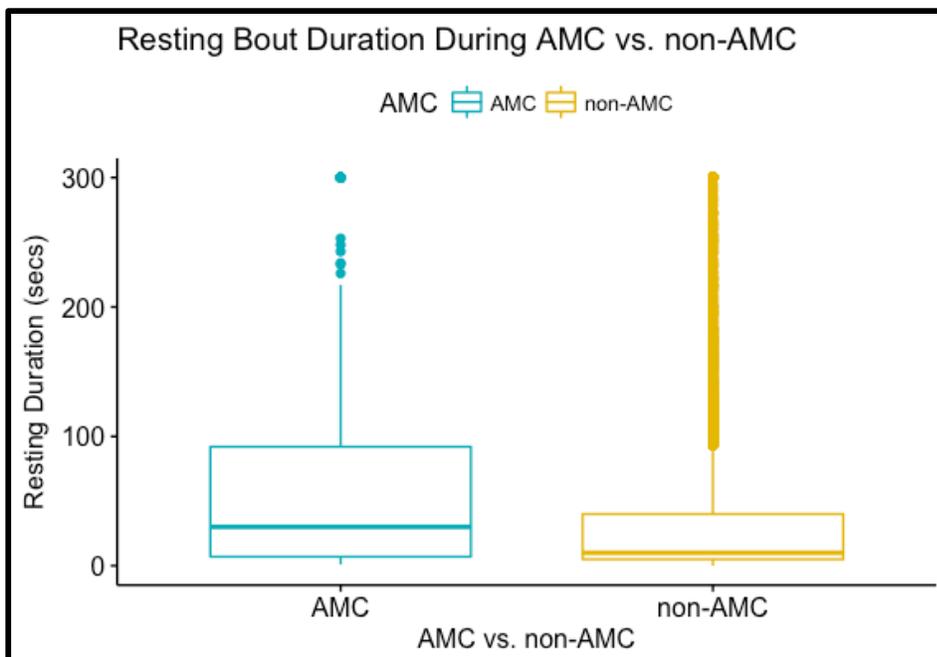

Figure 8. Resting Bout Duration During AMC vs. Non-AMC. AMC vs. non-AMC are listed on the x-axis and resting bout duration in seconds is on the y-axis. AMC vs non-AMC are delineated in the boxes by color.

The top five plant species consumed by each group differed slightly between groups, however the number one plant species consumed was the same for all three groups: *Celtis durandii* (see Table 9).

Table 9. *Top five plant species consumed by each group*

Group	Kasembo	Tail	Bingi
Plant Species	*Celtis durandii* (45%)	*Celtis durandii* (51%)	*Celtis durandii* (47%)
	Spatheodia (6.8%)	*Markhamia* (14.1%)	*Markhamia* (17.7%)
	Albizia (5.8%)	*Strychnosmitis* (9.1%)	*Celtis africana* (15.6%)
	Celtis africana (5.8%)	*Olea* (5.3%)	*Strychnosmitis* (7.2%)
	Markhamia (4.7%)	*Celtis africana* (4.6%)	*Olea* (2.3%)

The rate that a mother fed was compared between feeding bouts that took place during AMC and feeding bouts that took place during non-AMC. There was no significant difference between feeding rate during feeding bouts that took place during AMC and feeding bouts that took place during non-AMC (Wilcoxon rank-sum, $p > 0.05$). There was no significant difference between ME consumption rates for feeding bouts that took place during AMC vs. feeding bouts that took place during non-AMC (Wilcoxon rank-sum, $p > 0.05$).

Discussion

The results regarding maternal activity budgets showed that mothers are spending their time without their infants feeding more than any other activity. Similarly, the results supported my hypothesis by revealing that lactating mothers spend the majority of their time with their infants engaged in infant care, decreasing the amount of time they can spend on feeding, foraging, and resting. Furthermore, mothers feed and rest for longer durations during feeding and resting bouts that take place during AMC vs. non-AMC. The results between groups were

consistent with little variation. These results are a clear reflection of the burden of infant care.

Gestation, lactation, and carrying are all energetically taxing states for mothers (Altmann, 1980;

Gittleman & Thompson, 1988). Peak lactation can increase energy expenditure by 150%

(Gittleman & Thompson, 1988). Carrying an infant both physically constrains a mother's

movement and foraging capacity due to the extra weight load. The negative effects of infant

carrying on feeding frequency have been shown in other species (Altmann, 1980; Lappan, 2009).

Mothers in many species address this loss of energy by increasing feeding, using stored energy,

or reducing their energy expenditure in other activities, such as social interactions or travel

(Dunbar & Dunbar, 1988). Mothers may also switch to higher quality food sources or reduce

their activity levels during peak lactation (Pereira, 1993; Sauther, 1994).

     Similar trends are found in other species. Wild siamangs (*Symphalangus syndatcylus*)

have two energetically costly periods of infant care – lactation and carrying (Lappan, 2009) The

first 4-6 months of infant care are marked by the energetic cost of lactation, and the next 7-12

months are marked by the energetic cost of infant carrying (Lappan, 2009). Siamang mothers

tend to increase their rest during the lactation period and increase their feeding during the post-

lactation period (Lappan, 2009). Infant carrying is particularly taxing in the Callithrix family and

Tarsius genus, as infants are born weighing nearly half of their mother's weight (Fite et al.,

2005; Gursky, 2000). Similar to siamangs, marmosets, tamarins, and tarsiers spend time without

their infants resting and feeding (Fite et al., 2005; Gursky, 2000; Hrdy, 2016). It is thought that

tarsiers increase their resting and feeding intake to offset the cost of infant carrying and lactation,

much like siamangs (Gursky, 2000). However, for marmosets and tamarins, the increased

feeding and resting during AMC bouts are thought to shorten inter-birth intervals and maximize

reproductive output (Fite et al., 2005; Hrdy, 2016). Marmosets and tamarins have shorter life

histories than siamangs and tarsiers, and thus need to produce offspring at a higher frequency (Fite et al., 2005; Hrdy, 2016). Much like the siamangs and tarsiers, *C. guereza* have adopted a mixed strategy of feeding more and resting more when given the opportunity to offset the energetic costs of infant care during AMC bouts.

AMC occurred less than often reported in captive *C. guereza* infant care and more often than reported in wild *C. guereza* infant care (Harris, 2004; Horwich & Manski, 1975; McKenna, 1979). Yet, we found no difference between feeding rate and ME consumed for feeding bouts that took place during AMC vs. feeding bouts that took place during non-AMC. We only followed mothers and infants for 9 hours per day, thus our sampling is made up of far more non-AMC events than AMC events. This is not to say that AMC does not play an important role for *C. guereza* in energy replenishment during infant care. Out of all of the maternal feeding time recorded, 12.5% took place during AMC bouts. Although not statistically significant, 12.5% of all maternal feeding took place when mothers were not physically burdened with their infants. This is impressive when you consider that AMC makes up less than 5% of all maternal time. Anecdotally, and compared to other black-and-white colobus species, mothers rarely resisted infant handling attempts by conspecifics (Bădescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007). During several AMC bouts, mothers in this study transferred their infants to other group members to *initiate* AMC bouts. Infant transfer on the part of mothers has not yet been recorded in this species and indicates that AMC plays an important role in allowing mothers to feed without their infants. Mothers fed and rested more during AMC bouts than non-AMC bouts, and fed and rested for longer durations during AMC bouts than non-AMC bouts. From these results it is evident that maternal activity budgets change during AMC bouts, which implies that there are energetic benefits to *C. guereza* mothers who use AMC.

Results revealed that juvenile females handle infants more often than any other age-sex class. Juvenile females in all three groups were frequent infant handlers, babysitters, and play-partners. Nearest neighbor age, sex, and distance to mother are all significant predictors for the occurrence of AMC in *C. guereza*. The nearest neighbor to an infant can serve as a proxy for who is available to act as a helper to lactating mothers. Juvenile females were the nearest neighbor to infants more often than adult females. This is a trend seen throughout the primate order, including in other species of black-and-white colobus monkeys (Bădescu, Sicotte, Ting, & Wikberg, 2015). Nulliparous *Colobus vellerosus* showed more natal attraction and infant handling than adult females in Boabeng-Fiema Monkey Sanctuary, Ghana (Bădescu et al., 2015). Increased juvenile female helping behavior makes sense couched in the context of the learning-to-mother hypothesis. Infant care on the part of juvenile females may be adaptive, allowing them to fine-tune their maternal skills before they are reproductively mature (Lancaster, 1971). However, this learning process does not come without its failings. It's been noted that nulliparous females are not as careful or vigilant while infant handling than adult helpers may be (Bădescu et al., 2015; Lancaster, 1971). One infant in the Kasmebo group disappeared four months into the study. Although the cause of this infant's disappearance has not been confirmed, the infant was last seen being handled by a juvenile female. Infants in previous studies of *C. guereza* have died at the hands of careless helpers before (Harris, 2004; Oates, 1977).

Distance to mother is an expected predictor for AMC because infants must be away from mothers to be handled by a conspecific. When an infant was 3-5 meters away from its mother, AMC was more likely to occur. During this study, infants became distressed when their mothers traveled away from them and would vocalize in high-pitch squeals (Raboin, personal observation). Further research is needed on the vocalizations of *C. guereza*, but these infant

vocalizations could entice helpers to approach, huddle, groom, and carry infants to a location closer to their mother. The farther away a mother travels from its infant, the more an infant vocalizes, and thus the more an infant receives infant care from conspecifics.

Infant age and weather are not significant predictors of the occurrence of AMC. Weather was used as a potential predictor variable to tease apart any differences in infant handling between the wet and dry seasons. The results showed that there is no significant difference in the occurrence of infant handling between sunny, cloudy, rainy, and sunny/cloudy weather. This is not surprising, as *C. guereza* still travel, feed, rest, and engage in social behavior during the wet season at similar frequencies as during the dry season (Dunbar & Dunbar, 1976; McKenna, 1979; Oates, 1977).

Based on the existing literature of AMC in *C. guereza* and other black-and-white colobus species, infant handling occurs most often in the first four months of life, possibly due to the occurrence of infant natal coat color (Bădescu et al., 2015; Brent, Lauren; Teichroeb, Julie; Sicotte, 2007; Harris, 2004; McKenna, 1979; Oates, 1977). However, this study saw consistent occurrences of AMC from 1-10 months of infant age. Infant age was not a significant predictor of the occurrence of AMC, but it was a significant predictor of the duration of AMC bouts. This could be due to a number of reasons, such as increased infant foraging, increased infant independence, or helper preference of age, as infants grow and develop. These results show that AMC occurs at a regular frequency throughout infancy in its entirety in *C. guereza*, differing from other black-and-white colobus monkeys.

Future Directions

Gestation, lactation, and carrying infants causes infant care to be the most energetically taxing period in a female primate's life. Infant carrying physically constrains mother from

feeding and foraging due to the added weight load during travel. AMC, care of offspring by conspecifics, allows *C. guereza* mothers to offset the cost of infant care by entrusting the care of their infants to other group members. This should be further investigated through a longitudinal study that examines the role of the "learning-to-mother" hypothesis, investigates infant vocalizations as potential predictors of AMC, and includes a larger sample size of more groups in diversified habitats. A more robust energetic analysis would be useful to better understand how much energy mothers save by feeding and resting during AMC bouts.

References

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3–4),

227–266. https://doi.org/10.1163/156853974X00534

Altmann, J. (1980). Ecology and maternal time budgets. *Baboon Mothers and Infants %7 5*.

Bădescu, I., Sicotte, P., Ting, N., & Wikberg, E. C. (2015). Female parity, maternal kinship,

infant age and sex influence natal attraction and infant handling in a wild colobine (Colobus

vellerosus). *American Journal of Primatology*, *77*(4), 376–387.

https://doi.org/10.1002/ajp.22353

Bădescu, I., Watts, D. P., Katzenberg, M. A., & Sellen, D. W. (2016). Alloparenting is associated

with reduced maternal lactation effort and faster weaning in wild chimpanzees. *Royal

Society Open Science*, *3*(11), 160577. https://doi.org/10.1098/rsos.160577

Baldovino, M. C., & Di Bitetti, M. S. (2008). Allonursing in tufted capuchin monkeys (Cebus

nigritus): Milk or pacifier? *Folia Primatologica*, *79*(2), 79–92.

https://doi.org/10.1159/000108780

Bales, K., Dietz, J., Baker, A., Miller, K., & Tardif, S. D. (2000). Effects of Allocare-Givers on

Fitness of Infants and Parents in Callitrichid Primates. *Folia Primatologica*, *71*(1–2), 27–

38. https://doi.org/10.1159/000021728

Balshine-Earn, S., Neat, F. C., Reid, H., & Taborsky, M. (1998). Paying to stay or paying to

breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding

fish. *Behavioral Ecology*, *9*(5), 432–438. https://doi.org/10.1093/beheco/9.5.432

Beaudrot, L. H., Kahlenberg, S. M., & Marshall, A. J. (2009). Why male orangutans do not kill

infants. *Behavioral Ecology and Sociobiology*, *63*(11), 1549–1562.

https://doi.org/10.1007/s00265-009-0827-1

Bergmuller, R., Heg, D., & Taborsky, M. (2005). Helpers in a cooperatively breeding cichlid

stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the*

Royal Society B: Biological Sciences, *272*(1560), 325–331.

https://doi.org/10.1098/rspb.2004.2960

Bergmüller, R., Johnstone, R. A., Russell, A. F., & Bshary, R. (2007). Integrating cooperative

breeding into theoretical concepts of cooperation. *Behavioural Processes*, *76*(2), 61–72.

https://doi.org/10.1016/j.beproc.2007.07.001

Biben, M. (1992). Allomaternal vocal behavior in squirrel monkeys. *Developmental*

Psychobiology. https://doi.org/10.1002/dev.420250202

Borries, C., Launhardt, K., Epplen, C., Epplen, J. T., & Winkler, P. (1999). Males as infant

protectors in Hanuman langurs (Presbytis entellus) living in multimale groups - defence

pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology*, *46*(5), 350–

356. https://doi.org/10.1007/s002650050629

Brent, Lauren; Teichroeb, Julie; Sicotte, P. (2007). Preliminary Assessment of Natal Attraction

and Infant Handling in Wild Colobus vellerosus. *American Journal of Primatology*,

1222(70), 101–105. https://doi.org/10.1002/ajp

Briga, M., Pen, I., & Wright, J. (2012). Care for kin: within-group relatedness and allomaternal

care are positively correlated and conserved throughout the mammalian phylogeny. *Biology*

Letters, *8*(4), 533–536. https://doi.org/10.1098/rsbl.2012.0159

Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C., & Russell, A. F. (2012). Kin

selection, not group augmentation, predicts helping in an obligate cooperatively breeding

bird. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1743), 3861–3869.

https://doi.org/10.1098/rspb.2012.1080

Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male

primate society. *Nature*, *425*(6954), 179–181. https://doi.org/10.1038/nature01866

Bull, Ni. J., & Schwarz, M. P. (1997). Rearing of Non-Descendant Offspring in an Allodapine

Bee, Exoneura bicolor Smith (Hymenoptera: Apidae: Xylocopinae): A Preferred Strategy or

Queen Coercion? *Australian Journal of Entomology*, *36*(4), 391–394.

https://doi.org/10.1111/j.1440-6055.1997.tb01491.x

Burkart, J. M., & van Schaik, C. P. (2009). Cognitive consequences of cooperative breeding in

primates? *Animal Cognition*, *13*(1), 1–19. https://doi.org/10.1007/s10071-009-0263-7

Burkart, J. M., & van Schaik, C. P. (2016). Revisiting the consequences of cooperative breeding.

Journal of Zoology, *299*(2), 77–83. https://doi.org/10.1111/jzo.12322

Calegaro-Marques, C., & Bicca-Marques, J. C. (1993). Allomaternal Care in the Black Howler

Monkey (Alouatta caraya). Folia Primatologica.

Caperos, J. M., Sánchez, S., Peláez, F., Fidalgo, A., & Morcillo, A. (2011). The Effect of

Crowding on the Social Behavior of the Cooperatively Breeding Cotton-Top Tamarins

(Saguinus oedipus). *International Journal of Primatology*, *32*(5), 1179–1189.

https://doi.org/10.1007/s10764-011-9534-7

Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., & Zanne, A. E. (1999).

Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of

Tropical Ecology*, *15*(2), 189–211. https://doi.org/10.1017/S0266467499000759

Chism, J. (2000). Allocare patterns among cercopithecines. *Folia Primatologica*, *71*, 55–66.

https://doi.org/10.1159/000021730

Clarke, M. R., Glander, K. E., & Zucker, E. L. (1998). Infant-Nonmother Interaction of Free-

Ranging Mantled Howlers (Alouatta palliata) in Costa Rica. International Journal of

Primatology.

Clutton-Brock, T. (2002). Breeding Together: Kin Selection and Mutualism in Cooperative

Vertebrates. *Science*, *296*(5565), 69–72. https://doi.org/10.1126/science.296.5565.69

Cockburn. (1998a). Evolution of helping behavior in cooperatively breeding birds.

Ann.Rev.Ecol.Syst., *29*(1998), 141–177. https://doi.org/10.1146/annurev.ecolsys.29.1.141

Cockburn, A. (1998b). Evolution of Helping Behavior in Cooperatively Breeding Birds. *Annual

Review Ecological Systems*, *29*(1998), 141–177.

https://doi.org/10.1146/annurev.ecolsys.29.1.141

Cockburn, A., & Russell, A. F. (2011). Cooperative breeding: A question of climate? *Current

Biology*, *21*(5), R195–R197. https://doi.org/10.1016/j.cub.2011.01.044

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild

chimpanzees and orangutans: methodological considerations and a preliminary comparison.

Cambridge Studies in Biological and Evolutionary Anthropology, *48*(48), 445–472.

Cox, C. R., Tappan, J., & Engelhardt, H. (1987). Parental care and development of the red uakari

(Cacajao calvus rubicundus). American Journal of Primatology.

Davies, A. G. (1994). Colobine populations. In *Colobine monkeys: their ecology, behaviour and

evolution* (pp. 285–310).

Díaz-Muñoz, S. L. (2016). Complex cooperative breeders: Using infant care costs to explain

variability in callitrichine social and reproductive behavior. *American Journal of

Primatology*, *78*(3), 372–387. https://doi.org/10.1002/ajp.22431

Dunbar, R. I. M., & Dunbar, E. P. (1976). Contrasts in social structure among black-and-white

colobus monkey groups. *Animal Behaviour*, *24*(1), 84–92. https://doi.org/10.1016/S0003-

3472(76)80102-9

Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, *36*(4), 970–980. https://doi.org/10.1016/S0003-3472(88)80055-1

Dunham, N. T., & Opere, P. O. (2016). A unique case of extra-group infant adoption in free-ranging Angola black and white colobus monkeys (Colobus angolensis palliatus). *Primates*, *57*(2), 187–194. https://doi.org/10.1007/s10329-016-0515-5

Eberle, M., & Kappeler, P. M. (2006). Family insurance: Kin selection and cooperative breeding in a solitary primate (Microcebus murinus). *Behavioral Ecology and Sociobiology*, *60*(4), 582–588. https://doi.org/10.1007/s00265-006-0203-3

Ekman, J., & Ericson, P. G. . (2006). Out of Gondwanaland; the evolutionary history of cooperative breeding and social behaviour among crows, magpies, jays and allies. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1590), 1117–1125. https://doi.org/10.1098/rspb.2005.3431

Erb, W. M., & Porter, L. M. (2017). Mother's little helpers: What we know (and don't know) about cooperative infant care in callitrichines. *Evolutionary Anthropology*, *26*(1), 25–37. https://doi.org/10.1002/evan.21516

Evans, K. J. E., Pavelka, M. S. M., Hartwell, K. S., & Notman, H. (2012). Do Adult Male Spider Monkeys (Ateles geoffroyi) Preferentially Handle Male Infants? *International Journal of Primatology*, *33*(4), 799–808. https://doi.org/10.1007/s10764-012-9610-7

Fernandez-Duque, E., Ju??rez, C. P., & Di Fiore, A. (2008). Adult male replacement and subsequent infant care by male and siblings in socially monogamous owl monkeys (Aotus azarai). *Primates*, *49*(1), 81–84. https://doi.org/10.1007/s10329-007-0056-z

Fite, J. E., Patera, K. J., French, J. A., Rukstalis, M., Hopkins, E. C., & Ross, C. N. (2005). Opportunistic mothers: Female marmosets (Callithrix kuhlii) reduce their investment in

offspring when they have to, and when they can. *Journal of Human Evolution*, *49*(1), 122–
142. https://doi.org/10.1016/j.jhevol.2005.04.003

Fragaszy, D. M., Baer, J., & Adam-Curtis, L. (1991). Behavioral Development and Maternal
Care in tufted capuchins and squirrel monkeys from birth through seven months.
Development Psychobiology.

Fruteau, C., van de Waal, E., van Damme, E., & Noë, R. (2011). Infant access and handling in
sooty mangabeys and vervet monkeys. *Animal Behaviour*, *81*(1), 153–161.
https://doi.org/10.1016/j.anbehav.2010.09.028

Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., & Tautz, D. (1999). Intracommunity
relationships, dispersal pattern and paternity success in a wild living community of Bonobos
(Pan paniscus) determined from DNA analysis of faecal samples. *Proceedings. Biological
Sciences / The Royal Society*, *266*(1424), 1189–1195.
https://doi.org/10.1098/rspb.1999.0762

Gilchrist, J. S. (2007). Cooperative behaviour in cooperative breeders: Costs, benefits, and
communal breeding. *Behavioural Processes*, *76*(2), 100–105.
https://doi.org/10.1016/j.beproc.2006.12.013

Ginther, A. J., & Snowdon, C. T. (2009). Expectant parents groom adult sons according to
previous alloparenting in a biparental cooperatively breeding primate. *Animal Behaviour*,
78(2), 287–297. https://doi.org/10.1016/j.anbehav.2009.04.020

Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction.
Integrative and Comparative Biology, *28*(3), 863–875. https://doi.org/10.1093/icb/28.3.863

Gursky, S. (2000). Allocare in a nocturnal primate: data on the spectral tarsier, Tarsius spectrum.
Folia Primatologica International Journal of Primatology, *71*(1–2), 39–54.

https://doi.org/21729

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Harris, T. R. (2004). Abstracts of AAPA Poster and Podium Presentations. *American Association of Physical Anthropology*, 109–110. https://doi.org/10.1002/ajpa.21502

Harris, T. R., & Chapman, C. A. (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, *48*(3), 208–221. https://doi.org/10.1007/s10329-006-0036-8

Hatchwell, B. J., & Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, *59*(6), 1079–1086. https://doi.org/10.1006/anbe.2000.1394

Horwich, R. H., & Manski, D. (1975). Maternal care and infant transfer in two species of Colobus monkey. *Primates*, *16*(1), 49–73.

Hrdy. (2009). Mothers and others: the evolutionary origins of mutual understanding. Cambridge, Massachusetts: Harvard University Press.

Hrdy, S. B. (1974). Male-male competition and infanticide among the langurs (Presbytis entellus) of Abu, Rajasthan. *Folia Primatologica*, *22*(1), 19–58. https://doi.org/10.1159/000155616

Hrdy, S. B. (2016). Variable postpartum responsiveness among humans and other primates with "cooperative breeding": A comparative and evolutionary perspective. *Hormones and Behavior*, *77*, 272–283. https://doi.org/10.1016/j.yhbeh.2015.10.016

Huchard, E., Alvergne, A., Féjan, D., Knapp, L. A., Cowlishaw, G., & Raymond, M. (2010). More than friends? Behavioural and genetic aspects of heterosexual associations in wild

chacma baboons. *Behavioral Ecology and Sociobiology*, *64*(5), 769–781.

https://doi.org/10.1007/s00265-009-0894-3

Huck, M., & Fernandez-Duque, E. (2012). Children of divorce: Effects of adult replacements on

previous offspring in Argentinean owl monkeys. *Behavioral Ecology and Sociobiology*,

66(3), 505–517. https://doi.org/10.1007/s00265-011-1297-9

Huck, M., & Fernandez-Duque, E. (2013). When Dads Help: Male Behavioral Care During

Primate Infant Development Item. https://doi.org/10.1007/978-1-4614-4060-4

Isler, K., & van Schaik, C. P. (2012). Allomaternal care, life history and brain size evolution in

mammals. *Journal of Human Evolution*, *63*(1), 52–63.

https://doi.org/10.1016/j.jhevol.2012.03.009

Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J., & Rothman, J.

M. (2017). Macronutrient balancing affects patch departure by guerezas (Colobus guereza).

American Journal of Primatology, *79*(4), 1–9. https://doi.org/10.1002/ajp.22495

Kokko, H., Johnstone, R. A., & Clutton-Brock, T. (2001). The evolution of cooperative breeding

through group augmentation. *Proceedings of the Royal Society B: Biological Sciences*,

268(1463), 187–196. https://doi.org/10.1098/rspb.2000.1349

König, B. (1997). Cooperative care of young in mammals. *Naturwissenschaften*, *84*(3), 95–104.

https://doi.org/10.1007/s001140050356

Lancaster, J. B. (1971). Play-mothering: The Relations between Juvenile Females and Young

Infants among Free-ranging Vervet Monkeys <i>(Cevcopithecus

aethiops</i><i>)</i> *Folia Primatologica*, *15*(3–4), 161–182.

https://doi.org/10.1159/000155377

Lappan, S. (2008). Male care of infants in a siamang (Symphalangus syndactylus) population

including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology*, *62*(8), 1307–1317. https://doi.org/10.1007/s00265-008-0559-7

Lappan, S. (2009). The effects of lactation and infant care on adult energy budgets in wild siamangs (Symphalangus syndactylus). *American Journal of Physical Anthropology*, *140*(2), 290–301. https://doi.org/10.1002/ajpa.21069

Lee, H. J., Heim, V., & Meyer, A. (2016). Genetic evidence for prevalence of alloparental care in a socially monogamous biparental cichlid fish, Perissodus microlepis, from Lake Tanganyika supports the "selfish shepherd effect" hypothesis. *Ecology and Evolution*, *6*(9), 2843–2853. https://doi.org/10.1002/ece3.2089

Lehmann, L., & Keller, L. (2006). The evolution of cooperation and altruism - A general framework and a classification of models. *Journal of Evolutionary Biology*, *19*(5), 1365–1376. https://doi.org/10.1111/j.1420-9101.2006.01119.x

Li, T., Ren, B., Li, D., Zhu, P., & Li, M. (2013). Mothering Style and Infant Behavioral Development in Yunnan Snub-Nosed Monkeys (Rhinopithecus bieti) in China. *International Journal of Primatology*, *34*(4), 681–695. https://doi.org/10.1007/s10764-013-9687-7

Lukas, D., & Clutton-Brock, T. (2012). Cooperative breeding and monogamy in mammalian societies. *Proceedings. Biological Sciences / The Royal Society*, *279*(1736), 2151–6. https://doi.org/10.1098/rspb.2011.2468

Lukas, & Clutton-Brock. (2012). Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1736), 2151–2156. https://doi.org/10.1098/rspb.2011.2468

Maestripieri, D. (1994a). Mother-Infant Relationships in Three Species of Macaques (Macaca

Mulatta, M. Nemestrina, M. Arctoides). I. Development of the Mother-Infant Relationship in the First Three Months. *Behaviour*, *131*(1), 75–96. https://doi.org/10.1163/156853994X00226

Maestripieri, D. (1994b). Social structure, infant handling, and mothering styles in group-living old world monkeys. *International Journal of Primatology*, *15*(4), 531–553. https://doi.org/10.1007/BF02735970

Manson, J. (1999). Infant handling in wild Cebus capucinus: testing bonds between females? *Animal Behaviour*, *57*(4), 911–921. https://doi.org/10.1006/anbe.1998.1052

McKenna, J. J. (1979). The evolution of allomothering behavior among colobine monkeys: Function and opportunism in evolution. *American Anthropologist*, *81*, 818–840. https://doi.org/10.1525/aa.1979.81.4.02a00040

McKenna, J. J. (1979). The evolution of allomthering behavior among colobine monkeys: Function and opportunism in evolution. *American Anthropologist*, *81*(4), 818–840. https://doi.org/10.1525/aa.1979.81.4.02a00040

Meehan, C. L., Quinlan, R., & Malcom, C. D. (2013). Cooperative breeding and maternal energy expenditure among aka foragers. *American Journal of Human Biology*, *25*(1), 42–57. https://doi.org/10.1002/ajhb.22336

Meier, C., Hemelruk, C. K., & Martin, R. D. (2000). Paternity determination, genetic characterization, and social correlates in a captive group of chimpanzees (Pan troglodytes). *Primates*, *41*(2), 175–183. https://doi.org/10.1007/BF02557798

Mitani, J. C., & Watts, D. (1997). The evolution of non-maternal caretaking among anthropoid primates: Do helpers help? *Behavioral Ecology and Sociobiology*, *40*(4), 213–220. https://doi.org/10.1007/s002650050335

Muroyama, Y. (1994). Exchange of Grooming for Allomothering in Female Patas Monkeys. *Behaviour*, *128*(1), 103–119. https://doi.org/10.1163/156853994X00064

Murray, C. M., Stanton, M. A., Lonsdorf, E. V., Wroblewski, E. E., & Pusey, A. E. (2016). Chimpanzee fathers bias their behaviour towards their offspring. *Royal Society Open Science*, *3*(11), 160441. https://doi.org/10.1098/rsos.160441

Nekaris, K. A. I. (2006). Social Lives of Adult Mysore Slender Lorises (Loris lydekkerianus lydekkerianus). *American Journal of Primatology*, *1222*(68), 1171–1182. https://doi.org/10.1002/ajp.20316

O'Brien, T. J., & Robinson, J. G. (2013). Allomaternal Care by Female Wedge-Capped Capuchin Monkeys : Effects of Age , Rank and Relatedness, *119*(1), 30–50.

Oates. (1977). The Social Life of a Black-and-white Colobus Monkey, Colobus guereza. *Z. Tierpsychology*, *60*, 1–60.

Oates, J. F. (1994). The natural history of African colobines. In *Colobine monkeys* (pp. 75–128).

Onderdonk, D. A. (2000). Infanticide of a Newborn Black-and-White Colobus Monkey (Colobus guereza) in Kibale National Park. *Primates*, *41*(2), 209–212. https://doi.org/10.1007/BF02557802

Packer, C., Lewis, S., & Pusey, A. E. (1992). A comparative analysis of non-offspring nursing. Animal Behaviour, 43.

Pan, W., Gu, T., Pan, Y., Feng, C., Long, Y., Zhao, Y., … Yao, M. (2014). Birth intervention and non-maternal infant-handling during parturition in a nonhuman primate. *Primates*, *55*(4), 483–488. https://doi.org/10.1007/s10329-014-0427-1

Paul, A. (1999). The socioecology of infant handling in primates: Is the current model convincing? *Primates*, *40*(1), 33–46. https://doi.org/10.1007/BF02557700

Pereira, M. E. (1993). Seasonal adjustment of growth rate and adult body weight in ring-tailed

　　lemurs. In *Lemur Social Systems and Their Ecological Basis* (pp. 205–221).

　　https://doi.org/10.1007/978-1-4899-2412-4_15

Pereira, M. E., & Izard, M. K. (1989). Lactation and care for unrelated infants in forest-living

　　ringtailed Lemurs. *American Journal of Primatology*, *18*(2), 101–108.

　　https://doi.org/10.1002/ajp.1350180204

Rabenold, K. N. (1990). Campylorhynchus wrens: the ecology of delayed dispersal and

　　cooperation in the Venezuelan savanna. In *Cooperative breeding in birds* (pp. 157–196).

　　https://doi.org/10.1017/CBO9780511752452.007

R Core team. (2015). R Core Team. *R: A Language and Environment for Statistical Computing.*

　　R Foundation for Statistical Computing , Vienna, Austria. ISBN 3-900051-07-0, URL

　　http://www.R-Project.org/.

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young

　　nonhuman primates: Learning what, where, and how to eat. *Evolutionary Anthropology*,

　　17(4), 189–201. https://doi.org/10.1002/evan.20180

Riedman, M. L. (1982). The Evolution of Alloparental Care and Adoption in Mammals and

　　Birds Author (s): Marianne L . Riedman Source : The Quarterly Review of Biology , Vol .

　　57 , No . 4 (Dec ., 1982), pp . 405-435 Published by : The University of Chicago Press

　　Stable URL :, *57*(4), 405–435.

Ross, C., & Regan, G. (2000). Allocare, predation risk, social structure and natal coat colour in

　　anthropoid primates. *Folia Primatologica; International Journal of Primatology*, *71*(1–2),

　　67–76. https://doi.org/10.1159/000021731

Rothman, J. M. (2018). *Unpublished data*.

Rothman, J. M., Chapman, C. A., & van Soest, P. J. (2012). Methods in Primate Nutritional Ecology: A User's Guide. *International Journal of Primatology*, *33*(3), 542–566. https://doi.org/10.1007/s10764-011-9568-x

Rotundo, M., Fernandez-Duque, E., & Dixson, A. F. (2005). Infant development and parental care in free-ranging Aotus azarai azarai in Argentina. *International Journal of Primatology*, *26*(6), 1459–1473. https://doi.org/10.1007/s10764-005-5329-z

Saito, A., Izumi, A., & Nakamura, K. (2011). Fathers have higher motivation for parenting than mothers in common marmoset (<I>Callithrix jacchus</I>). *Behaviour*, *148*(11), 1199–1214. https://doi.org/10.1163/000579511X596598

Sauther, M. (1994). Wild Plant Use by Pregnant and Lactating Ringtailed Lemurs, with Implications for Early Homid Foraging. In *Eating on the Wild Side: The Pharmacologic, Ecologic and Social Implications of Using Noncultigens* (pp. 240–256).

Schubert, M., Pillay, N., & Schradin, C. (2009). Parental and Alloparental Care in a Polygynous Mammal. *Journal of Mammalogy*, *90*(3), 724–731. https://doi.org/10.1644/08-MAMM-A-175R1.1

Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, *57*(Reidman 1982), 1021–1032. https://doi.org/10.1006/anbe.1998.1065

Silk, J. B. (2002). Kin Seletion in Primate Groups. *International Journal of Primatology*, *23*(4), 849–875.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*(1480), 539–559. https://doi.org/10.1098/rstb.2006.1994

Slater, K. Y., Schaffner, C. M., & Aureli, F. (2007). Embraces for infant handling in spider

monkeys: evidence for a biological market? *Animal Behaviour*, *74*(3), 455–461.

https://doi.org/10.1016/j.anbehav.2006.11.026

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. https://doi.org/10.1002/evan.20132

Stanford, C. B. (1992). Costs and benefits of allomothering in wild capped langurs (Presbytis

pileata). *Behavioral Ecology and Sociobiology*, *30*(1), 29–34.

https://doi.org/10.1007/BF00168591

Sutton, G. J., Hoskins, A. J., & Arnould, J. P. Y. (2015). Benefits of group foraging depend on

prey type in a small marine predator, the little penguin. *PLoS ONE*, *10*(12).

https://doi.org/10.1371/journal.pone.0144297

Tecot, S. R., Baden, A. L., Romine, N., & Kamilar, J. M. (2013). Reproductive strategies and

infant care in the malagasy primates. In *Building Babies: Primate Development in

Proximate and Ultimate Perspective* (pp. 321–359). https://doi.org/10.1007/978-1-4614-

4060-4_15

Tiddi, B., Aureli, F., & Schino, G. (2010). Grooming for infant handling in tufted capuchin

monkeys: a reappraisal of the primate infant market. *Animal Behaviour*, *79*(5), 1115–1123.

https://doi.org/10.1016/j.anbehav.2010.02.008

Trivers, R. L. L. (1972). Parental investment and sexual selection. *Sexual Selection and the

Descent of Man*. https://doi.org/10.1002/ajpa.1330400226

Xiang, Z. F., Sayers, K., & Grueter, C. C. (2009). Direct paternal care in black-and-white snub-

nosed monkeys. *Journal of Zoology*, *278*(2), 157–162. https://doi.org/10.1111/j.1469-

7998.2009.00563.x

Yao, M., Yin, L., Zhang, L., Liu, L., Qin, D., & Pan, W. (2012). Parturitions in Wild White-Headed Langurs (Trachypithecus leucocephalus) in the Nongguan Hills, China. *International Journal of Primatology*, *33*(4), 888–904. https://doi.org/10.1007/s10764-012-9625-0

Young, A. J., Carlson, A. a, Monfort, S. L., Russell, A. F., Bennett, N. C., & Clutton-Brock, T. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences*, *103*(32), 12005–12010. https://doi.org/10.1073/pnas.0510038103

Zhao, Q., Tan, C. L., & Pan, W. (2008). Weaning age, infant care, and behavioral development in Trachypithecus leucocephalus. *International Journal of Primatology*, *29*(3), 583–591. https://doi.org/10.1007/s10764-008-9255-8