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Allomaternal Care and Juvenile Foraging among the Hadza: Implications for the Evolution of Cooperative Breeding in Humans

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Anthropology

by

Alyssa Noelani Crittenden

Committee in charge:

Professor Margaret Schoeninger, Chair
Professor James Moore
Professor Lawrence Palinkas
Professor Cheryl Rock
Professor Shirley Strum

2009

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The dissertation of Alyssa Noelani Crittenden is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California, San Diego

2009

DEDICATION

This dissertation is dedicated to my grandparents, Nellie and Victor Calvo, my brother, Duncan Fastabend, and my mother, Suzanna Calvo. Their strength, wisdom, humor, and unrelenting support have sustained me.

EPIGRAPH

The true Promethean spirit of science means to liberate man by giving him knowledge and some measure of dominion over the physical environment. But at another level and in a new age, it also constructs the mythology of scientific materialism, guided by the corrective devices of the scientific method, addressed with precise and deliberately affective appeal to the deepest needs of human nature, and kept strong by the blind hopes that the journey on which we are now embarked will be further and better than the one just completed.
~ E.O. Wilson *On Human Nature* (1978)

Life knocked me off my platforms, so I pulled out my first pair of boots and suited up for the long walk back to myself, closer to the ground now with sorrow and stealth.
~ ani difranco

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ACKNOWLEDGEMENTS

I would like to thank the Department of Anthropology and the Friends of the International Center at the University of California, San Diego and the National Science Foundation (grants #9529278 and #0544751 to Frank W. Marlowe) for research funding and support and COSTECH in Tanzania for research permission. I would also like to thank Dave Zes at the Center for Environmental Statistics at the University of California, Los Angeles for assistance with the programming language R; Jackie Benjamin for her perseverance, good humor, and friendship; Lee Sei Hwan (UCSD), Tiffany Abramson (Harvard), Mike Bowen (Harvard), and Aradhana Tiwari (UCSD) for their hard work; Lene and Johannes Kleppe for their generous hospitality; and my Tanzanian research assistants Happy Msofe, Golden Ngumbuke, Danny Ngumbuke, Ephraim Mutukwaya, and Pastory Bushozi for their dedication and companionship. I am grateful for assistance and encouragement provided by the office of the Anthropology department, including Jenni Lewis, David Marlowe, Theresa Blankenship, Nikki Gee, JC Krause, and Kae Knight, and the Center for Academic Research and Training in Anthropogeny (CARTA), including Linda Carlson, Amy Patterson, Pascal Gagneux, and Ajit Varki; and the kids on the hall: Kyleb Wild, Beth Peterson, Andrew Somerville, Andy Froehle, Nicole Barger, and Angelica Marcello for their support and encouragement while in the trenches.

I am greatly indebted to Frank Marlowe for introducing me to the Hadza and for his mentorship and continuous support; Nancy Lou Conklin-Brittain for invaluable and lab instruction, wonderful hospitality, and never-ending patience; Jim and Sue Moore (and the entire Moore menagerie – especially Ben and Maeve!) for

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I would like to thank Brigitte Barshay, Michelle Mallen, Anna McColl, Tori Heflin, Coren Apicella, Raquel Calvo, Lucy Rutherford, Kate James and Kelli Kuehner for their encouragement and laughter. I am forever grateful and privileged to have the support and companionship of my boyfriend and best friend, Brian Dawidowicz. I would also like to thank my mother, Suzanna Calvo, for her patience, encouragement and friendship; my brother, Duncan Fastabend, for his constant good humor and solidarity; my grandmother, Nellie Calvo, for her support and guidance; and my grandpa, Victor Calvo, whose life long love of biology, natural history, ecology, and conservation have been a great source of inspiration.

Chapter 2, in full, is a reprint of the material as it appears in *Human Nature* volume 19, 2008. The dissertation author was the primary investigator and author of this paper. Chapter 3, in part, is currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this paper. Chapter 4, in part, is currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this paper.

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Crittenden, A.N. (2008) Cooperative Care among the Hadza Foragers of Tanzania. Paper presented at the Society for Anthropological Sciences Annual Meeting, New Orleans, Louisiana.

Crittenden, A.N. and F.W. Marlowe (2006) The Helping Behavior of Hadza Children: Childcare and the Evolution of Cooperative Breeding in Humans. Invited Session: Cultural Dimensions of Kin Investment: The Foundations of Kinship and Family. Paper presented at the Evolutionary Anthropology Society, American Anthropological Association Annual Meeting, San Jose, California.

Crittenden, A.N. and F.W. Marlowe (2006) Alloparenting among the Hadza of Tanzania. Paper presented at the Seventy-Seventh Annual Meeting of the American Association of Physical Anthropologists, Anchorage, Alaska.

Crittenden, A.N. (2004) Diet Composition and Differential Foraging Strategies of Hadza Men and Women. Paper presented at Session 2A Quantitative Data and Time Series Methods, the 4th Annual Graduate Research Symposium, University of California San Diego.

Crittenden, A.N., Richardson, M.R., Schoeninger, M.J., Bunn, H.T., and Pickering, T.R. (2003) Differential Foraging Strategies and Diets of Hadza Men and Women. American Journal of Physical Anthropology 120(S36), poster to be presented at the Seventy-Second Annual Meeting of the American Association of Physical Anthropologists.

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Photo: *Thirst Quencher – Hadza hunter-gatherers dig tubers for water* by A.N. Crittenden
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Body Ornamentation: Artistic Representations of Self ~ Photo Exhibit
San Diego Museum of Man, San Diego California (www.museumofman.org)
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ABSTRACT OF THE DISSERTATION

Allomaternal Care and Juvenile Foraging among the Hadza:

Implications for the Evolution of Cooperative Breeding in Humans

By

Alyssa Noelani Crittenden

Doctor of Philosophy

University of California, San Diego 2009

Professor Margaret J. Schoeninger, Chair

Human females have unique life history traits when compared to other apes including early weaning of infants and a shortened inter-birth interval (IBI). The current study explores the mechanisms that allow human females to successfully have more closely spaced births and support multiple dependents by testing the Cooperative Breeding hypothesis, which suggests that group members other than the biological mother (allomothers) assist in rearing offspring. Behavioral data on the frequency of holding

children and ecological data on self-provisioning among juvenile foragers is used to explore aspects of cooperative caregiving and provisioning among the Hadza hunter-gatherers of Tanzania. The results indicate that although mothers spend the largest amount of time in direct care of their infants and young children, additional categories of caregivers routinely provide investment. Related caregivers spend the largest percentage of time holding children, which supports kin selection (or nepotism) as the strongest motivation to provide allomaternal care. In addition to behavioral investment, the current study determines the extent to which juveniles offset the high cost of their own care by provisioning themselves. The results suggest that Hadza children begin foraging for various types of plant and animal foods starting at the age of five years. A wide variation in returns is seen across all young foragers in the sample, however some individuals are able to collect 50 – 70% of their daily needs. The flexibility of the human foraging niche creates an opportunity for juvenile food collection that alleviates constraints on maternal investment. Taken together, the results of this study suggest that juvenile foraging and nepotistic investment are two mechanisms that allow mothers to maintain a short inter-birth interval while supporting multiple dependent children, lending support to the Cooperative Breeding hypothesis.

I. Human Life History and the Cooperative Breeding Hypothesis

The Human Life History Pattern

When compared to other apes, humans have unique life history traits that include a longer potential life span, late age at first birth, short inter-birth interval (IBI), early weaning, and a prolonged juvenile period (Table 1) (Charnov & Berrigan 1993; Robson et al. 2006). Humans have a relatively slow life history and a life span that exceeds that of the other great apes by decades (Charnov & Berrigan 1993). It has been suggested that species with slow life histories tend to wean later and have longer IBI (Robson & Wood 2008), yet human reproduction is characterized by the early weaning of infants, before they are nutritionally independent, and a short IBI (Hawkes et al. 1997; Kaplan et al. 2000, 2001). This pattern is not only novel among apes, but also differs from the typical mammalian pattern.

Age at weaning

In general, most mammal infants are weaned when they reach one third of their mother's body weight or when the first permanent molar erupts (Charnov & Berrigan 1993; Lee et al. 1991). If humans followed this pattern, weaning would occur between

6 and 6.5 years (Smith 1991, 1992; Lee et al. 1991) rather than the typical pattern seen across human populations where infants are weaned between 1.5 – 2.5 years of age (Table 1) (Alvarez 2000; Kennedy 2005).

Table 1: Life history variables of female great apes - wild populations of non-human primates and human foraging populations

Species	Age at first reproduction (years)	Age at weaning (years)	Inter-birth Interval (years)
Orangutan (*Pongo* sp.)	15.6 [1]	7 [2]	8.05 [2]
Gorilla (*Gorilla* sp.)	10 [2]	4.1 [3]	4.4 [2]
Chimpanzee (*P. troglodytes*)	13.3 [4]	4.5 [2]	5.46 [5]
Bonobo (*P. paniscus*)	14.2 [6]	NA	6.25 [7]
Human (*H. sapiens*)	19.5 [8]	2.8 [2,9]	3.69 [10]

[1] Wich et al. 2004
[2] Alvarez 2000
[3] *G. beringei* 3.6 years (Fletcher 2001); *G. gorilla* 4.6 years (Nowell & Fletcher 2007)
[4] Bossou 10.9 years (Sugiyama 2004); Gombe 13.3 years (Wallis 1997); Kibale 15.4 years (Wrangham in Knott 2001); Mahale 14.56 years (Nishida et al. 2003); Tai 13.7 years (Boesch & Boesch-Achermann 2000)
[5] Bossou 5.3 years (Sugiyama 2004); Budongo 5.6 years (Brewer-Marsden et al. 2006); Gombe 5.2 years (Wallis 1997); Kanywara, Kibale 5.4 years (Brewer-Marsden et al. 2006); Mahale 5.6 years (Nishida et al. 2003); Tai 5.7 years (Boesch & Boesch-Achermann 2000)
[6] Kuroda 1989
[7] Lomako 8 years (Fruth in Knott 2001)
[8] Ache 19.5 years (Hill & Hurtado 1996); Hadza 18.77 (Blurton Jones unpublished and Marlowe personal communication); Hiwi 20.5 years (Kaplan et al. 2000); !Kung 19.2 years (Howell 1979)
[9] Kennedy 2005
[10] Ache 3.2 years (Hill & Hurtado 1996); Hiwi 3.76 years (Kaplan et al. 2000); !Kung 4.2 years (Howell 1979)

Age at first reproduction

Humans tend to have a relatively late age at first reproduction (average ages range between 18 and 20 years of age) when compared to other apes (Table 1). Cross culturally and across subsistence regimes, there is only modest variation in the age at

first reproduction (Bogin 2008; Martin et al. 2003), which may indicate the limited flexibility in this human life history trait (Robson & Wood 2008). A late age at first reproduction permits slow growth over a longer period of development (Janson & van Schaik 1993; Purvis & Harvey 1995). Mammals with slow life histories also tend to have larger body sizes, which means that they can, in turn, produce larger (and more energetically expensive) infants (Stearns 1992; Hawkes 2006; Robson & Wood 2008). Slow human life history means slow maturation.

Prolonged Juvenile Period

Humans are also distinct from other apes in that the human life history pattern includes the insertion of the "novel growth period" of childhood (Bogin 1997, 2008). Lengthened periods of juvenility in humans may be an evolutionary byproduct of selection on longer life-spans in general (Blurton Jones & Marlowe 2002; Charnov & Berrigan 1993; Leigh 2001; Pagel & Harvey 1993) or may be linked to the increased demands of learning a wealth of information prior to adulthood (Bogin 1997; Kaplan et al. 2000).

Raising Multiple Energetically Expensive Children

Human mothers wean their infants before they are nutritionally independent, allowing them to resume ovulation sooner and have subsequent offspring more rapidly, effectively shortening IBI (Hawkes et al. 1997, Kaplan et al. 2000). A shortened IBI allows women to give birth to new infants while simultaneously providing care for existing children, allowing human females to rear a greater percentage of offspring to adulthood when compared to other apes (Bogin 1997; Bogin & Smith 1995). Human infants are energetically expensive, however, and require provisioning and other types of high investment care for a decade or longer (Bogin 2008).

Young infants subsist entirely on mother's milk, and when an infant is weaning they must be provided with foods that are easily digestible and energetically rich (Bogin 2008). Older children, although they may eat some of the foods consumed by adults, are constrained by the type of food that their immature dentition and digestive systems can process (Bogin 2008; Kramer 2005a). It requires nearly 13 million kilocalories to raise a single infant from birth to nutritional independence and such requirements go far beyond what a mother can procure alone (Hrdy 2005b, 2009; Kaplan 1994; Kramer 2005a).

Mothers are faced with the unique problem of providing care to unweaned infants while simultaneously maintaining their economic production to successfully feed older children (Hill and Kaplan 1988; Hrdy 1999, 2009; Kramer 2005a; Le Vine et al. 1996; Panter-Brick 1989). It has been suggested that mothers accomplish the feat of provisioning multiple young by relying on other group members who release them from some of the energetic burden of reproduction by caring for or provisioning their infants (Bove et al. 2002; Hawkes et al. 1997; Hrdy 2005a; Ivey 2000; Kramer 2005 a,b; Meehan 2005). Investment from individuals other than the biological mother (allomothers) may increase a mother's fertility and/or the survivorship of her children (Bereczkei & Dunbar 1997, 2002; Crognier et al. 2001, 2002; Flinn 1989; Ivey 2000; Sear et al. 2000, 2002; Turke 1988). It has been proposed that reliance on allomaternal support is a central characteristic of human life history and that humans evolved as cooperative breeders (Hrdy 1999; 2009). The current study tests the Cooperative Breeding hypothesis to determine the extent of allomaternal care among the Hadza hunter-gatherers of Tanzania.

The Cooperative Breeding Hypothesis

Cooperative breeding is defined as "a breeding system in which group members other than the genetic parents (alloparents) help one or both parents rear their offspring" (Hrdy 2005a,b). Due to difficulties in assigning paternity certainty, the term "allomother" is more frequently used (Hrdy 2005b). The Cooperative Breeding hypothesis suggests that allomaternal assistance, in the form of behavioral investment (e.g. childcare) or food provisioning, is a derived characteristic of the genus *Homo* and was critical to infant survival during the Pleistocene. This breeding system, which is markedly different from extant apes, would have allowed hominid females to successfully produce multiple costly infants without increasing IBI (Hrdy 2009). Hominids would most likely have been living under conditions of high mortality (Kurland & Sparks 2003) and children with access to allomaternal care may be more likely to survive (Hrdy 2005b; Kennedy 2005). Shared care of young would also have allowed early hominids to effectively exploit new habitats.

The theoretical explanation typically used to explain allomaternal investment is Hamilton's Rule, which states that an individual might be expected to help another whenever the benefit to the recipient is greater than the cost to the helper divided by the degree of relatedness between them (Hamilton 1964). Allomothers may gain

inclusive benefits from helping their kin, however even unrelated individuals may be motivated to invest in young and thereby gain potential benefits such as increased strength in social bonds or access to care (i.e. reciprocity) (Clutton-Brock 2002; Emlen 1991; Hamilton 1964).

The cooperative breeding system is flexible and permits mothers to produce multiple dependent young at a faster rate by relying on the support of both kin members and unrelated helpers. Humans have a slow life history coupled with a fast rate of reproduction; this could only have evolved in a setting where mothers could depend on reliable assistance in rearing their offspring.

Aim of the Current Study

The current study tests the Cooperative Breeding hypothesis among the Hadza hunter-gatherers of Tanzania. The frequency of holding children is used as a measure of direct investment to identify the constellation of caregivers available to an infant or young child and the extent to which they provide care. Kin selection, or nepotistic investment, is frequently employed as the primary motivation to provide care under the Cooperative Breeding model. The kin selection hypothesis is tested to determine if

individuals tend to more frequently hold infants with whom they are more closely related.

In addition, ecological data on the foraging behavior of juveniles, a typically underrepresented class of caregiver, is used to determine the extent to which young foragers provision themselves. Juveniles are an interesting class of allomother to explore because they do not have any dependent infants of their own to care for and may therefore provide substantial assistance (Kramer 2005a; Robson et al. 2006). Previous reports on the daily food collection of juvenile hunter-gatherers are largely anecdotal. The current study expands our understanding of the characteristics of juvenile foraging and provides the first detailed report that quantifies the ways in which young foragers attenuate the cost of their own care. The Hadza are an ideal population in which to study the evolution of cooperative breeding because they live in a communal setting, practice no form of birth control, do not participate in a market economy, and live in an ecological environment that may have been quite similar to that of our early hominid ancestors.

The Hadza

The Hadza are hunter-gatherers who live in a savanna-woodland habitat east of Lake Eyasi in Northern Tanzania (Figure1). Approximately 300 individuals, out of a total population of 1000, practice a strictly hunting and gathering way of life. They live in camps with approximately 30 individuals, although camp composition is fluid and people often move in and out. Frequent movement between camps is common and is attributed to the fact that the Hadza do not traditionally recognize land rights and ownership of natural resources (Kaare 1994; Woodburn 1968). The average population size has not significantly grown in the last 100 years, although there has been a trend towards staying in larger camps for longer periods of time due to many areas being taken over by non-Hadza tribes (Fosbrooke 1956; Marlowe 2002; McDowell 1981).

Figure 1: Map of Hadza Research Area

Camps move approximately every two months in response to the seasonal availability of water and foods (Marlowe 1999; Woodburn 1968). Distinct wet and dry seasons associate with differential subsistence behaviors and social arrangements (Hawkes et al. 1989; Vincent 1985; Woodburn 1968). During the dry season, which lasts roughly from June through October, camp size is relatively large. The larger aggregation of people during the dry season may be due to the limited availability of water and/or the greater availability of animals concentrated near watering holes (Bunn et al. 1988; Woodburn 1968). During the wet season, which lasts roughly from November to May, camp size is smaller and may be linked to more freely available drinking water (Woodburn 1968).

Hadza foraging is characterized by a distinct sexual division of labor. Women forage in groups and primarily focus on gathering plant foods such as baobab fruit, berries, and underground tubers. Men typically forage alone, collecting baobab fruit and several types of honey, as well as hunting a wide variety of birds and mammals. Nursing infants accompany their mothers on daily foraging trips, however when a child is approximately 2-3 years old and being weaned, they are typically left in camp

with others. Children may be left without adult supervision but typically remain under the charge of at least one elderly camp member or an older juvenile caregiver.

Hadza Childhood

Young children are raised in a communal setting. In camp, children often play in large mixed age and mixed sex groups. Children's play includes games, dolls made out of mud or cloth, target practice, or digging tubers (Blurton Jones 1993). Children are weaned on ground baobab powder, animal fat, pre-masticated meat, and honey. Once weaned, children spend a considerable amount of time foraging and tend to focus on easy to collect foods that are located close to camp (Blurton Jones 1993); they may acquire up to 50% of their daily intake by age 5 (Blurton Jones et al. 1989). In addition to foraging for their own consumption, they also provision their younger siblings or other younger children left in their charge.

Children may accompany their mothers on foraging excursions or forage in mixed age and sex parties of children unaccompanied by an adult. Female children and adolescents almost always forage in groups, whereas male children tend to abandon the group foraging parties and begin solo foraging trips around the age of ten

years. During this time they are given bows and arrows that function quite well; bows given to Hadza children of younger ages are small in size and often times unusable, similar to the "toy" bows given to children of various other hunting populations (Gusinde 1931; Healey 1990; MacDonald 2007 for review; van Beek 1987; Watanabe 1975).

Receiving a functioning bow and fletched arrows occurs simultaneously with the adolescent growth spurt among the Hadza that is characterized by marked increases in skill and development of muscular specialization due to increases in height and strength (Harrison et al. 1993; Parker 1984; Walker et al. 2006). Up until this point, young male children tend to limit their hunting play to the confines of camp where they play with miniature bows and arrows and practice shooting very small prey such as mice. As they mature, the size and precision of their bows and arrows matures with them and they begin to target larger prey such as hyrax and large birds such as hornbills. These features appear to characterize juvenile hunting across cultures (Bock and Johnson 2004; Gusinde 1931; Healey 1990; Lancy 1996; Lee 1979; Marshall 1976; MacDonald 2007 for review; Ray 1963; van Beek 1987; Watanabe 1975).

Outline of Study

Chapter two investigates the extent to which various individuals invest in the offspring of others by analyzing who holds children while in camp and tests the kin selection hypothesis. Chapter three analyzes the nutrient content of foods collected by juvenile foragers in order to determine their potential energy contributions. Chapter four analyzes data on food acquisition among Hadza children and adolescents to explore general characteristics of juvenile foraging across seasons and the average food returns of young foragers from various age classes. Contributions from juvenile foraging underwrite the cost of care and may contribute to a mother's ability to successfully raise multiple dependents. Chapter five summarizes results and discusses implications for the evolution of cooperative breeding in humans.

II. Kin Selection and Nepotistic Investment

Several hypotheses have been proposed to account for cooperative care (Cockburn 1998; Emlen and Wrege 1989; Hamilton 1964; Wright 1997). Nepotistic investment (kin selection) appears to be the most common form of cooperative care (Hrdy 1999; Ivey 2000; Kramer 2005; McKenna 1987; Meehan 2005). Hamilton's rule states that an individual might be expected to help another whenever $B > C/r$, where B = the benefit to the recipient, C = cost to the helper, and r = the degree of relatedness between them (Hamilton 1964). Helpers may often stand to gain indirect fitness benefits, giving them higher inclusive fitness, by caring for closely related young (Clutton-Brock 2002; Emlen 1991, 1988; Reyer 1984; Russell and Hatchwell 2001; Skutch 1987). In some species of cooperative breeders, helpers may also gain direct benefits in the form of limited access to a mate, or they may exchange help for acceptance into a group that provides them greater protection from predation (Cockburn 1998; Clutton-Brock 2002).

Among humans, where a wide range of related and unrelated adult, adolescent, and child helpers contribute care, the costs and benefits of helping may involve various tradeoffs depending on the age and reproductive status of the caregiver

(Kramer 2005). Helping is facultative and if the cost of helping is too high, allomothers may not provide care (Hrdy 2005b). When allomothers can gain from helping kin, one should expect that their investment will be greater when the degree of relatedness to the recipient child is higher. A handful of studies among human populations have found a correlation between the degree of genetic relatedness of the helper and the amount of care provided (Denham 1974; Hames 1988; Ivey 2000).

Previous analyses have shown that although Hadza mothers spend the most time in direct childcare, children also receive a considerable amount of care from a wide range of helpers (Marlowe 2005). The current study identifies the array of allomaternal caregivers among the Hadza and tests the kin selection hypothesis using holding children as a measure of direct care.

Methods

Data were collected in ten camps over seventeen months of fieldwork from 1995 – 2004 (see Figure 1 for map of research area). The data from 1995 – 2003 were collected by Dr. Frank W. Marlowe (Florida State University) and subsequently

analyzed by the author and Dr. Marlowe. The data from 2004 were collected and analyzed by the author.

Holding was measured by conducting hourly instantaneous scan observations from sunrise to sunset (13 per day) in which the behavior of every individual in camp was recorded. Holding (from the holder's perspective) and being held (from the child's perspective) were both analyzed. When referring to 'being held' the unit of analysis is the child; when referring to 'holding' the unit of analysis is the allomother. Although holding/being held does not offer a complete picture of cooperative care, it is an easily quantifiable behavior that can be energetically demanding (Kramer 1998; Mitani and Watts 1997), as well as essential in keeping infants from hurting themselves, for example by falling or getting burned in a hearth.

It is very rare for children over four years of age to be routinely held because they are heavy and fairly independent. For this reason, only children four years of age and younger are used in this analysis. Holders <18 years old were designated as "juveniles" and holders $\geq$18 years were designated as adults. The behavior of all individuals present in camp during a camp scan was recorded. Although 13 scans were performed daily, there was considerable variability in the number of scans conducted

per camp, thus per individual. Large camps required longer stays in order to collect other behavioral and ecological data. There was also variation in the amount of time people resided in a camp as well as in the number of scans in which they appeared, which was largely due to how much time they were out of camp foraging.

Percent of time holding/being held was calculated by dividing numbers of observations of holding/being held by the total number of scans that an individual appeared in (i.e. being present in camp). However, only individuals appearing in at least 10 scans were used in the analysis. This allowed for the exclusion of cases in which visitors were holding a child in the one and only scan that they appeared in, which would result in the misleading impression that some people hold 100% of the time.

Counts of observations of holding/being held were also analyzed using non-parametric tests, weighting more heavily the cases for which the number of observations was greater (see Appendix 1). In every instance the results were confirmed. The presented analysis has the advantage of being able to control for covariates such as the age and sex of the child.

Household membership and kin affiliation were determined by censuses and interviews in each camp. Ages were estimated and then corroborated with long-term census data from Nicholas Blurton Jones (1982-1994) and Frank W. Marlowe (1995-2004). Using these data, which include reproductive histories, all relatives of each category residing in the same camp as the child were identified.

Eighteen relationship categories were initially coded for holding behavior (relationship between holder and holdee). These included: mother; father; maternal and paternal grandparents, aunts, uncles, and cousins; distantly related kin; and unrelated individuals. Only biological fathers were coded as father – stepfathers were coded as unrelated. An individual was classified as a "distant relative" if they were more distantly related than first cousin. To make categories more manageable for the initial descriptive statistics, the relationships that accounted for < 1% of the time a child was being held was assigned to the category "other kin" which includes: maternal and paternal grandfathers, paternal aunt, maternal and paternal cousins, and distant relatives. A .5 degree of relatedness includes fathers and full-siblings, .25 includes grandparents, half-siblings, aunts, and uncles, and .125 includes cousins. Proportions of time a child was held by categories of all persons with each degree of

relatedness were also determined. All holding by mothers, including holds when the mother was nursing, were included in the initial descriptive analyses. However, because the aim of this study is to determine the extent of allomaternal care, holding by mother was excluded in all subsequent analyses.

The residence of the allomother was controlled for in the following comparisons: when determining if being held was a product of kin selection (comparison of time being held by degrees of relatedness), maternal versus paternal kin, and maternal grandmothers versus paternal grandmothers. When determining if the degree of relatedness between holder and child correlated with the amount of time a child was held, only the holds where children had at least one representative from each category of relatedness (.5, .25, and .125) living in camp were included. In order to control for residence of maternal and paternal kin, only children who had at least two maternal and paternal kin members living in camp were included in the analyses.

A multivariate linear regression model that controlled for the age and sex of the child was used when determining if the three categories of degree-of-relatedness to the child decreasingly (from .5 to .125) predicted proportions of time being held. For these, standardized betas are reported. The Wilcoxon signed rank test for related

samples was used when the child being held was the unit of analysis. For example, the Wilcoxon signed rank was used to test whether children were held more by all kin than all non-kin, or by all maternal kin than all paternal kin, or by the maternal grandmother than the paternal grandmother. Mann-Whitney U tests were used when the unit of analysis was the holder, for example to test whether female allomothers held more than male allomothers.

Results

A total of 470 individuals (n_1 = 234 females, n_2 = 236 males) were represented in 42,031 person scans. The sample included a total of 68 children four years old and younger (n_1 = 28 females, n_2 = 40 males), out of which 74% were held (n_1 = 25 females, n_2 = 31 males); all children four years of age or younger were included in the analyses, whether they were observed being held or not. A total of 185 individuals were observed holding (n_1 = 132 females, n_2 = 53 males), of these 46 were mothers and 139 were allomothers. Of the total time Hadza children were held, 69% of the time they were held by their mother and 31% by allomothers (Table 2), who ranged in age from 1.5 - 79 years old.

Table 2: Percentage of the total time (100%) that children < 4 years of age

Relationship Category	n	Mean % Time Being Held	Mean % Time Being Held When Controlling for Residency in Camp
Mother	46	68.7	68.9
Father	34	7.1	9.4
Older Sister	56	1.2	2.8
Maternal Grandmother	16	3.7	9.5
Paternal Grandmother	8	1.2	6.1
Maternal Aunt	33	1.9	3.5
Other Kin	*	3.6	*
Unrelated	77	12.4	*
Total		100	100

* The values for "Other kin" and "Unrelated" could not be calculated because they represent overlapping categories and individuals may appear multiple times, making it impossible to control for residence in camp

A child's age is, of course, a strong and significant predictor of the proportion of time he/she is held, with younger children held more ($\beta = -.762$, $p < .0005$, d.f. = 66, $R^2 = .575$, $n_1 = 28$ females, $n_2 = 40$ males) (Figure 2). For this reason, child's age is controlled in all tests where the child is the unit of analysis. The sex of a child (males = 1, females = 2) was not associated with the proportion of time a child was held, controlling for age ($\beta = .040$, $p = .747$, d.f. = 66, $R^2 = -.014$, $n_1 = 28$ females, $n_2 = 40$ males).

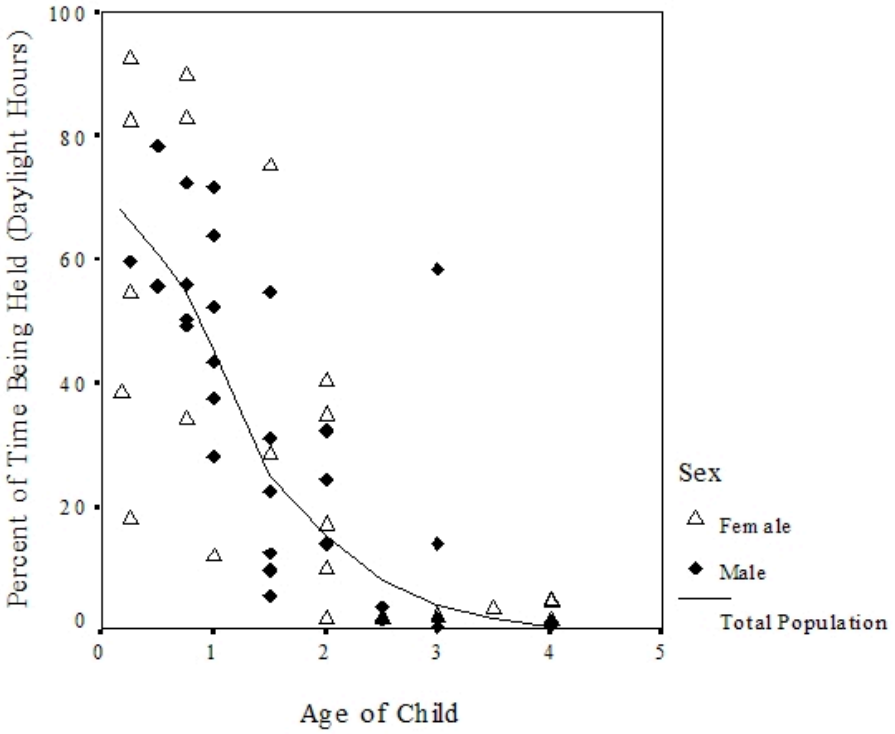

Figure 2: Percent of time children <4 years of age were being held

Across holders of all ages, females spent more time holding children than males (Figure 3), but the difference was not quite significant (Mann-Whitney U = 1862.00, p = .080, n_1 = 52 males and n_2 = 87 females). Juveniles aged 1.5 – 17.9 years old represented 62% of the total allomothers (n_1= 44 females, n_2 = 12 males) (Figure 4, the lines show locally weighted averages smoothed with a Lowess fit). Female juvenile allomothers far outnumbered their male counterparts and spent a significantly greater proportion of their time holding children (Mann-Whitney U = 130.5, p = .008,

$n_1 = 44$ females, $n_2 = 12$ males). Figure 4 reveals that holding by girls is highest between eight and twelve years of age.

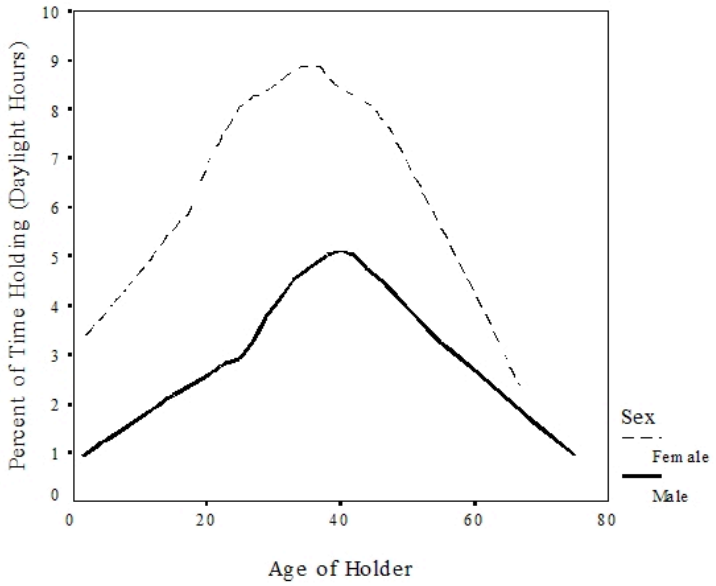

Figure 3: Percent of time spent holding children <4 years of age (including mothers)

Children were held by related allomothers (all kin members including distantly related) significantly more than by unrelated allomothers (Wilcoxon signed rank $Z = -2.439$, $p = .015$, $n_1 = 62$ related, $n_2 = 77$ unrelated). In order to determine if categories of degree-of-relatedness (all holding by relatives with that degree-of-relatedness lumped together) between the holder and the child were significant predictors of percent time being held, a multiple linear regression controlling for the age and sex of

the child was run. The total proportion of time the child was held was the dependent variable and excluded all holding done by mothers. The three categories of degree-of-relatedness between the holder and the child were all significant but decreasingly strong predictors of percent time being held: .5, ($\beta = .784$, $p < .005$), .25, ($\beta = .489$, $p < .005$), and .125, ($\beta = .127$, $p < .005$; final model, d.f. = 67, $R^2 = .980$, $p < .005$). Figure 5 also shows that a higher degree of relatedness between the holders and the child associates with a higher mean percent time being held.

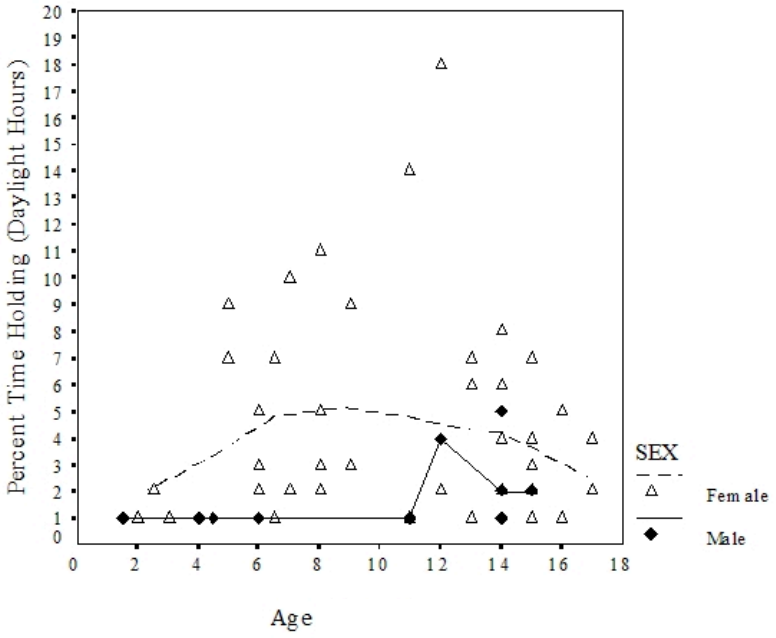

Figure 4: Percent of time spent holding by juvenile allomothers

Although related individuals spent more time holding, children were held overall by unrelated helpers 12.4% of the time. This is more than any other single category of allomother (Table 2). Among unrelated helpers (n_1 = 65 females, n_2 = 12 males) there was no significant difference between adults and juveniles in the amount of time spent holding (Mann-Whitney U 1670.5, p = .185, n_1= 28 juveniles, n_2= 49 adults).

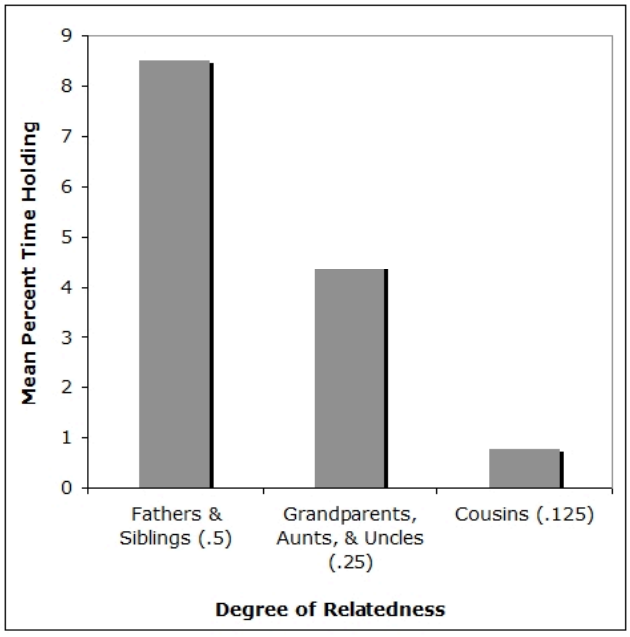

Figure 5: Mean percent of time spent holding by allomothers by degree of relatedness to the child

Children were held more by maternal relatives than paternal relatives when controlling for residency in camp (Wilcoxon signed rank Z = -2.808, p = .005, n_1= 78 maternal kin, n_2 = 46 paternal kin). However, maternal grandmothers did not hold significantly more than paternal grandmothers (Wilcoxon signed rank Z = -1.079, p = .281, n_1= 28 maternal grandmothers, n_2 = 11 paternal grandmothers). Camp residence for grandmothers is biased in that paternal grandmothers only tend to live with their grandchildren when their son is still married to the child's mother while maternal grandmothers are much more likely to live with their grandchildren when the father (her daughter's husband) does not still live with the child. The residence of fathers and maternal grandmothers was inversely related (Spearman's Rank Correlation r_s = -.400, p < .005, n = 68 children), whereas the residence of fathers and paternal grandmothers was positively related (Spearman's Rank Correlation r_s = .259, p = .027, n = 68 children).

Discussion

There is a considerable amount of allomaternal care among the Hadza provided by a wide range of individuals. Mothers account for the bulk of time a child is being

held, supporting Konner's (2005) assertion that mothers are the primary caretakers among hunter-gatherers. This study agrees with previous findings among the Aka (Meehan 2005) and the Hadza (Marlowe 2005), which show that there is no direct correlation between a high frequency of allomaternal support and a reduction in the frequency of maternal investment. This is perhaps due to a mother's limited ability to reduce time spent in childcare due to the specific demands of nursing (Kramer 2005). Mothers may be benefiting from allomaternal care in other ways, such as trading childcare and/or holding responsibilities, or via not-in-kind reciprocity with mothers providing food to allomothers in exchange for their help.

Both fathers and grandmothers provide a substantial amount of allocare. Residence patterns in this study support previous research suggesting that a woman will depend more on her mother when her husband is absent and vice versa (Blurton Jones et al. 2005; Marlowe 2005). Hadza couples more frequently reside with the wife's kin (Blurton Jones et al. 2005; Woodburn 1968), and a higher number of maternal relatives appear to be routinely available to provide care (Table 2). When comparing maternal versus paternal kin, maternal relatives hold more frequently. However, this does not extend to grandmothers; when both are in residence there is no

significant difference between the amount of time maternal and paternal grandmothers are holding.

Maternal grandmothers have been shown to positively affect outcomes such as survivorship and growth of their grandchildren (Bereczkei 1998; Hawkes 1997; Hawkes et al. 1989; Leonetti et al. 2002, 2005; Mace and Sear 2005). Conversely, paternal grandmothers are expected to invest less than maternal grandmothers, a reflection of lower paternity certainty than maternity certainty (Euler and Weitzel 1996). The current study shows no difference in grandmaternal frequency of holding. This suggests that the Hadza may have high paternity confidence, that paternal grandmothers may choose to live with particular sons who are more likely to have high paternity confidence, or that paternity confidence is not the most significant variable influencing grandmaternal residence choices. The tendency for older women to reside in the same camp with their daughters more often than their sons could be partially influenced by maternity confidence in their daughters' children.

Related allomothers spend significantly more time holding children when compared to unrelated helpers. Relatives contribute care in proportion to their degree of relatedness to the recipient child; holding frequency is greater when the degree of

relatedness to the recipient child is higher. Although the results are significant, suggesting that among the Hadza, nepotism is a primary motivation for providing allomaternal care, a causal relationship between relatedness and level of care is not necessarily confirmed. Investment from kin may derive from the fact that kin tend to co-reside, which creates the opportunity for helping (Griffin and West 2002). Of course, the probability that kin co-residence itself is favored by kin selection should not be discounted (Foster, Wenseleers, and Ratnieks 2006).

Juvenile allomothers (Figure 6) may spend up to 20% of their time in camp holding both related and unrelated children. Children and adolescents routinely provide care and "babysit" younger children, as is seen across many cultures and subsistence regimes (for review see Barry & Paxson 1971; Hewlett & Lamb 2005; Werner 1984; Zellar 1987). The substantial amount of childcare assistance routinely provided by juvenile helpers is well documented and is argued to be one of the ways that mothers offset their time constraints (Bove 2002; Borgerhoff-Mulder & Milton 1985; Denham 1974; Ivey et al. 2005; Konner 1977; Kramer 2005a; Munroe et al. 1984; Nag et al. 1978; Weisner & Gallimore 1977; Whiting & Whiting 1975; Zellar 1987). The time and energy that children and adolescents spend in food collection,

however, is far less documented (Kramer 2005a). It may be that children make their most substantial allomaternal contribution by way of self-provisioning. The following chapters will address the extent to which juvenile foragers among the Hadza subsidize their own growth and maintenance.

Figure 6: Juvenile allomothers holding their younger siblings

Chapter 2, in full, is a reprint of the material as it appears in *Human Nature* volume 19, 2008. The dissertation author was the primary investigator and author of this paper.

III. Nutrient Composition of Juvenile Foods

Research among young foragers has provided insight into the complex relationship between various subsistence regimes and the feasibility of children's work (Bliege Bird & Bird 2002; Blurton Jones et al. 1989; Blurton Jones & Marlowe 2002, Bock 2002; Draper & Cashdan 1988; Hawkes et al. 1995; Kaplan 1997; Kramer 2002, 2005a; Zeller 1987). The extent to which children and adolescents collect their own food is dependent on both the type of foods available and the constraints associated with participation in food collection tasks (Kramer 2005a). In environments that are both safe (i.e. have low predator pressure and are located close to water) and contain foods that are easy to locate and acquire close to camp, children may spend a considerable amount of time each day collecting food (Bird & Bliege Bird 2005; Bliege Bird & Bird 2002; Blurton Jones et al. 1989, 1994, 1997; Chowning 1972; Draper & Cashdan 1988; Dwyer 1972; Hawkes et al. 1995; Kaplan et al. 2000; Kramer 2005 a,b; Tucker & Young 2005; Turke 1988). Although anecdotal data suggests that in these environments children may be able to substantially contribute to their own daily energy requirements, this is the first study to quantify overall daily collection among a large sample of juvenile hunter-gatherers.

In order to successfully estimate the ways in which juvenile foraging may benefit a mother who is raising multiple dependent offspring, the chemical composition and energy values for juvenile foods must be determined. The current study analyzes several of the key foods collected by Hadza children and adolescents. Young foragers target a wide variety of plant and animal foods that are available year round. There is no consensus as to the seasonal availability of foods, due in large part to the inter- and intra-annual variability of rainfall; however, during the dry season, medium- to large-sized game animals, berries, tubers, and baobab are generally available. During the wet season, small-sized game animals, honey and bee larvae, tubers, and baobab are available (Blurton Jones el al. 1991; Bunn et al. 1988; Hawkes et al. 1989; Marlowe 2007; Vincent 1984; Woodburn 1968).

Relatively few studies on the nutrient composition of plant foods in the Hadza diet have been done. The three published studies, Murray et al. 2001, Schoeninger et al. 2001, and Vincent 1984, provide data on the macronutrient composition of eight species of plant foods consumed by the Hadza. The current study includes re-samplings of four of those species and an analysis of seven new plant species, including foods collected only by juvenile foragers.

Methods

Field Collection

Plant foods were collected in four Hadza camps during the summer of 2001 (camp Mang'ola) the summer of 2004 (camp Mang'ola), spring of 2005 (camp Gangidape), and fall of 2005 (camp Siponga). A Hadza forager collected each food sample; thus, each sample is representative of the foods typically consumed. In most cases, the samples were taken from a fraction of the collection that the individual forager would bring back to camp each day to feed their families. Food is not always abundant; therefore, only small samples (approximately ten grams dry weight) were available for analysis. A total of eighty-five samples from twenty-four types of food were obtained for analysis, which provided replicate sampling of several species. The current study focuses only on juvenile foods, therefore only a portion of the above samples, twenty-six samples from eleven types of food, are reported here.

The consumed and unconsumed portion of each food was collected, separated into various parts (i.e. pulp, seed, husk), and subsequently dried in an open air-drying rack. Whenever possible, the samples were dried in the shade. In some camps, however, there was little to no shade in which to dry the samples and in these instances the samples were dried in the sun. Macronutrient analysis does not

necessitate shade drying, as does the analysis of micronutrients or secondary plant compounds. The drying rack was constructed out of wood, stood two feet off of the ground, and had a wire mesh top to allow the air to dry the samples. Due to the fact that all samples were air-dried, the temperature at which the samples dried was dependent on the ambient outdoor temperature. The drying temperatures never exceeded 38 degrees Celsius. During inclement weather (e.g. dry season dust storms or wet season rainstorms) the samples were moved indoors to limit contamination. Some foods, primarily berries and figs, have a high sugar content which made them more susceptible to molding, especially during the rainy season. These samples were closely monitored and moved to the driest region of the rack or indoors. Once the samples were dry, they were placed in manila envelopes and stored.

Types of Plant Foods

The berry species reported in this analysis (*Cordia senensis* and *Salvadora persica)* have proportionately large seeds with very little pulp. When consuming the berries, the seeds are either expectorated or passed through the digestive system with little or no physical alteration. All berries are consumed raw, either fresh (off of the

plant) or slightly dried (stored for a few days). The seeds were extracted from the pulp during field processing, and the resulting pulp was dried, stored, and then analyzed.

Baobab fruit (*Adansonia digitata*) is consumed throughout the year in great amounts. The fruit has a hard green outer capsule that comprises approximately 50% of the total weight of the fruit (Nour et al. 1980). During field processing, the outer capsule was weighed and subsequently discarded; only the inner pulp with seeds were dried and analyzed. The inside of the capsule is composed of approximately 12 – 20 seeds which are covered with dry, white, chalky pulp that may be consumed in four ways: (1) directly out of the capsule, discarding the hard seed inside the pulp, (2) pounded into a flour, removing the seeds by winnowing on the surface of small piece of animal hide, (3) combining the flour with water and/or berry juice to create a sweet paste that is used as a weaning food, or (4) removing the intact seeds from the dung of baboons, washing and then pounding into flour.

The one species of drupe in this analysis, Mashalobe (unknown *Genus species)*, has a very hard seed surrounded by dense pulp. This drupe cannot be consumed without first boiling it to render the pulp soft and pliable. Once boiled, the

pulp falls off of the hard seed and is consumed; the seed is discarded. Both the pulp and seed were collected and dried after boiling, however only the pulp was analyzed.

Figs (*Ficus sycomorus*) are a popular and highly desirable food mainly consumed by children and adolescents. They are collected in the early morning or late afternoon, in order to avoid competition with neighboring baboon troops who also consume this fruit. The figs are collected by picking them up off of the ground beneath the tree once they have fallen, or after shaking the tree vigorously to encourage the figs to drop to the ground. They are typically consumed whole, including the small seeds inside of the pulpy fruit. Occasionally some children will pick out the seeds and consume only the pulp of the fig.

Another food mainly consumed by juveniles is the legume species (*Acacia nilotica*), which is collected from acacia trees. The legumes look similar to domestic soybean pods. They are first boiled and then the pulse (the inner seed) is extracted from the outer covering and consumed. Both the covering and the pulses were collected; however, only the pulses were stored and analyzed.

Several species of tubers, underground storage organs (USOs), are routinely collected by women and juveniles. They have historically been considered central

energy sources, important alternatives to meat consumption, and an integral food in human evolution (Hawkes et al. 1989; Pennisi 1999; Wrangham et al. 1989; Vincent 1985). The majority of tubers collected by the Hadza are located up to 3 meters below the surface of the ground (Schoeninger et al. 2001; Vincent 1985) and are accessed using the sharpened tip of a digging stick (Figure 7). Tubers may be peeled and consumed raw or roasted unpeeled on a fire (Figure 8). When consuming *//Ekwa* (*Vigna frutescens*), the tuber is chewed for up to three minutes and then a quid is expectorated (Schoeninger et al. 2001). Before expelling the quid, the fibrous mass is sucked free of all moisture while still in the mouth. All portions of each tuber species (peel and pith) were collected, separated, and dried in the field. Only the inside pith was analyzed.

Figure 7: Woman digging //Ekwa tubers during the dry season

Figure 8: Roasting //Ekwa on a fire

Chemical Analysis

Chemical assays were performed by the author in the Nutritional Ecology Laboratory in the Anthropology Department at Harvard University. All foods were analyzed to determine the content of fat (lipid), crude protein (CP), free mono- and disaccharides, fiber (neutral-detergent fiber - NDF), and ash. Total non-structural carbohydrates (TNC) were determined by difference (see below).

Lipid content was determined using a petroleum ether extraction over four days at room temperature under a chemical hood. This is a modification of the method of the Association of Official Analytical Chemists (AOAC 1984); however, it follows the methods outlined in various analyses of wild African foods (Conklin & Wrangham 1994; Conklin-Brittain et al. 1998). The modification is designed to prevent the extraction of non-nutritional waxes and latexes.

Crude protein (CP) was determined using the Kjeldahl procedure for total nitrogen and then multiplied by 6.25 (Pierce & Haenisch 1947). The digestion mix combined $CuSO_4$ with the reagent Na_2SO_4. The receiving solution in the distillation was 4% boric acid that was titrated with 0.1 N HCl.

Free mono- and disaccharides were analyzed using a phenol/sulfuric acid calorimetric assay (Dubois et al. 1956) and modified using a sucrose standard (per Strickland and Parsons 1972).

Fiber was estimated using neutral-detergent fiber analysis (Van Soest 1994), which measures all of the insoluble fibers: cellulose, hemicellulose, and lignin. The NDF extraction was sequentially followed by the acid detergent fiber (ADF) extraction which solubilizes the hemicellulose (HC), and is determined by subtraction: NDF – ADF = HC. The ADF, which still contains cellulose and lignin, is then subjected to 72% sulfuric acid. This solubilizes the cellulose (Cs) which is also determined by subtraction: ADF – lignin (Ls) = Cs. The resulting residue contains only lignin (Ls).

Ash was measured by drying a subsample (< 1 gram) of each food at 100 degrees Celsius for eight hours and then hot weighing the crucible. The subsample was then ashed at 520 degrees Celsius for approximately eight hours and the crucible was again hot weighed at 100 degrees Celsius (AOAC 1984; Conklin & Wrangham 1994; Conkin-Brittain et al. 2006).

Total non-structural carbohydrates (TNC) were calculated using as follows: TNC = 100 - % NDF - % lipid - % CP - % ash (per Conklin-Brittain et al. 1998).

Energy values (total kilocalories) were determined for each food based on the potential energy contribution of the above listed nutrient fractions. Energy was calculated using 4 kcal/g dry matter (DM) for protein and total non-structural carbohydrates and 9 kcal/g DM for lipids (based on National Research Council 1989).

Results

All of the chemical values reported here are expressed as a percentage of the dry matter (DM) of each food, as opposed to a percentage of the organic matter, because these results are being compared to literature values that are expressed as %DM.

Fat Analysis

Among the five samples of baobab fruit (*Adansonia digitata*), the level of fat in the pulp is small (less than 2%), which agrees with previously published values for Hadza baobab pulp flour (Busson 1965; Murray et al. 2001). The baobab flour from

pulp and seed combined, however, has a relatively high fat content (see Table 3) and the values reported here are within the range of published values (Salami & Okezie 1994). The tafabe berry (*Salvadora persica*) has a high fat content of nearly 18%, whereas the undushabe berry (*Cordia senensis*) has a low value of less than 3%. There are no published values in which to compare the tafabe berry. The values for undushabe fall within range of published values (Murray et al. 2001). This is the first reported analysis of the legume mangwala (*Acacia nilotica*) and the drupe mashalobe (unknown species), both of which have small amounts of fat (<1%). The fig (*Ficus sycomorus*) has a relatively high fat content (approximately 10%), in spite of not containing seeds. This is slightly higher than the 2% - 7% fat reported for figs from Kibale National Park, Uganda (NL Conklin-Brittain, personal communication). All five species of tubers, four of which were analyzed for the first time, have a fat content of approximately ≤ 1% (see Table 4).

Protein Analysis

The baobab pulp has a low crude protein level (<4%), whereas the flour from the pulp and seed has a higher value (12 - 15%). The tafabe and undushabe berries

both have a crude protein level falling between 10% and 12%). The above results are well within range of published values (Murray et al. 2001). The legume mangwala has a high protein level (typical of legumes in general) of approximately 25%. The values for the drupe and fig are somewhat lower, <1% and 10% respectively. All five species of tubers have a protein level of ≤ 12%.

Carbohydrate Analysis

The free mono- and disaccharides for baobab range from 13 - 35%. Tafabe berry has a high free mono- and disaccharide content (~ 49%) whereas the undushabe berry has far less (29%, but still fairly sweet). The free mono- and disaccharide content of mangwala is low (7 - 9%) and the values for mashalobe and ogoyo (fig) are quite high, ~ 31% and ~34% respectively. The values for the tubers range from ~10% in makalita (*Rhynchosia comosa*) to ~ 23% in shaheako (*Vigna macrorhyncha*). The values reported here are within the range of the published values for previously analyzed species: baobab, berries, and tubers (Murray et al. 2001; Schoeninger et al. 2001).

Table 3: Macronutrient Content of Fruits, Berries, and Legumes (%DM)

Hadza name (English name) *Genus species*	Moisture %[2]	Lipid	Crude Protein (CP)	Free Mono- and Disaccharides	Neutral Detergent Fiber (NDF)	Acid Detergent Fiber (ADF)	Hemicellulose (HC)	Cellulose (Cs)	Lignin (Ls)	Total Non-structural Carbohydrates (TNC)	Ash	Kilocalories (kcal) /100 g dry matter (DM)[3]
N//obabe (Baobab)												
Adansonia digitata												
1 (pulponly)	57.2	0.6	3.5	35.1	15.1	9.7	5.4	7.4	2.3	79.7	6.0	339
2 (pulp only)	56.1	1.3	3.5	20.0	17.3	11.2	6.1	8.7	2.5	76.7	5.3	334
3 (pulp & seed)	56.8	12.1	13.0	16.5	38.4	28.0	10.3	17.3	10.7	26.1	13.9	292
4 (pulp & seed)	56.6	12.2	12.3	17.4	40.6	28.9	11.6	17.5	11.4	24.4	13.9	282
5 (pulp & seed)	55.3	9.2	14.9	13.0	44.4	31.1	13.3	20.7	10.4	28.0	4.9	262
Tafabe (Berry)												
Salvadora persica												
1	55.2	17.9	10.8	48.9	13.0	10.2	2.8	4.0	6.1	48.1	19.8	447.0
Undushabe (Berry)												
Cordia senensis												
1	60.7	2.9	11.6	29.0	39.0	35.2	3.7	22.3	12.8	36.5	15.8	232
Mangwala (Legume)												
Acacia nilotica												
1 (raw)	67.8	0.2	26.5	9.9	30.4	10.4	20.0	9.7	0.8	36.7	9.7	267
2 (cooked)	86.5	0.5	24.9	7.2	33.5	11.8	21.7	11.5	0.2	35.6	8.5	256
Mashalobe (Drupe)												
unknown *Genus species*												
1	54.5	0.1	7.8	30.6	45.9	43.5	2.3	19.5	23.9	46.3	10.1	217
Ogoyo (Fig)												
Ficus sycomorus												
1	23.6	10.3	3.4	34.1	29.3	24.8	4.6	13.4	11.4	53.8	7.0	329

[1] Dry weight totals do not add up to 100g because each value is an average of multiple analyses
[2] Moisture contents were determined by drying a subsample (< 1 gram) at 100 degrees Celsius for eight hours and hot weighing
[3] Energy was calculated using 4 kcal/g dry matter (DM) for protein and total non-structural carbohydrates and 9 kcal/g DM for lipid

Table 4: Macronutrient Content of Tubers (per 100g dry, peeled tuber)

Hadza name *Genus species* Sample number	Cooked or Raw	Moisture %[2]	Lipid	Crude Protein (CP)	Free Mono- and Disaccharides	Neutral Detergent Fiber (NDF)	Acid Detergent Fiber (ADF)	Hemicellulose (HC)	Cellulose (Cs)	Lignin (Ls)	Total Non-structural Carbohydrates (TNC)	Ash	Kilocalories (kcal) /100 g dry matter (DM)[3]
//Ekwa													
Vigna frutescens													
1	Raw	69.3	1.2	7.9	13.5	26.8	21.0	5.8	18.3	2.7	61.9	5.7	293
2	Raw	67.8	0.9	4.8	22.8	24.7	16.2	8.5	12.3	3.9	66.0	10.4	295
3	Raw	69.4	0.1	9.0	21.4	29.7	20.3	9.4	18.1	2.3	59.4	4.5	276
4	Raw	69.8	0.1	7.1	16.1	41.4	28.6	12.9	24.9	3.7	47.1	8.1	220
5	Cooked	67.7	1.8	7.6	12.2	31.6	16.1	15.5	13.5	2.5	56.1	6.4	275
6	Cooked	68.7	1.8	10.4	15.0	18.5	9.9	8.6	8.8	1.1	67.8	4.6	332
7	Cooked	69.3	0.4	5.9	14.5	42.6	25.4	17.3	21.9	3.6	46.0	9.2	215
8	Cooked	68.6	0.0	5.1	12.4	10.6	8.0	2.6	6.7	1.2	82.3	11.6	352
Shumuako													
Vatoraea pseudolablab													
1	Raw	88.7	0.8	3.0	12.1	34.7	28.3	6.4	18.1	10.2	50.8	30.7	225
2	Cooked	91.4	0.3	3.6	12.3	35.6	27.7	7.9	24.3	3.4	50.8	19.6	225
Makalita													
Rhynchosia comosa													
1	Raw	79.3	0.1	5.4	14.9	40.1	27.5	12.6	17.7	9.9	45.3	16.7	208
2	Raw	79.1	0.3	5.9	10.1	56.9	44.7	12.3	36.5	15.4	27.3	13.3	140
3	Cooked	79.3	0.5	5.1	14.6	43.0	29.3	13.7	22.4	6.9	39.7	19.3	190
Matukwaya													
Coccinea surantiaca													
1	Raw	86.5	0.0	12.4	23.1	13.3	8.8	4.4	7.5	1.3	69.5	15.7	337
Shaehako													
Vigna macrorhyncha													
1	Raw	85.7	0.6	10.4	22.9	22.4	14.4	8.0	12.1	2.3	58.6	19.5	292

[1] Dry weight totals do not add up to 100g because each value is an average of multiple anal;
[2] Moisture contents were determined by drying a subsample (< 1 gram) at 100 degrees Celsius for eight hours and hot weighing
[3] Energy was calculated using 4 kcal/g DM for protein and total non-structural carbohydrates and 9 kcal/g DM for lipid

The neutral-detergent fiber (NDF) content of baobab pulp flour is 15 - 17%, whereas the NDF contents of baobab pulp and seed flour are significantly higher, ranging from 38% to 44%. This wide range of fiber content agrees with previously published values for baobab (Addy & Eteshola 1984; Busson 1965; Murray et al. 2001). The tafabe berry has an NDF content of 13%, which is significantly less than the NDF content of the undushabe berry which is 39%, a value within range of published values (Murray et al. 2001). The legume, drupe, and fig all have high NDF content, ranging from 30% - 45% NDF. The wide range of NDF content among the tuber species agrees with previously published reports on the variability of fiber in wild tubers (Schoeninger et al. 2001). The values range from 13% in matukwaya (*Coccinea surantiaca*) to 43% in makalita (*Rhynchosia comosa*).

Energy Value

The energy value for each food was determined using 9 kcal/g DM for fat and 4 kcal/g DM for protein and carbohydrate, and expressed as kcal/100g dry matter (DM). The energy values for baobab pulp flour (334 kcal to 339 kcal) are slightly higher than those for pulp and seed flour (262 kcal to 292 kcal). All values fall within

the range of published values (Addy & Eteshola; Busson 1965; Salami & Okezie 1994: Murray et al. 2001). The energy value for tafabe berry (447 kcal) is the highest for all foods in the sample. The undushabe berry (232 kcal), the legume (256 kcal - 267 kcal) and drupe (217 kcal) are all within a similar range. The fig has a relatively high energy value of 329 kcal. The tuber species range from a low 140 kcal (makalita) to a high 337 kcal (matukwaya). These energy values are higher than previously published values for the same and similar species (Schoeninger et al. 2001: Vincent 1984, 1985).

Discussion

The results presented here agree with the previously published values, with one exception; in this analysis, the energy content of the tuber species has a higher upper range limit when compared to the two previous analyses (Schoeninger et al. 2001; Vincent 1985). This may be due to differences in field processing techniques. Schoeninger et al. 2001 only analyzed the edible portions of the tubers (and did not analyze the expectorated quid), whereas Vincent 1984, 1985 and this study analyzed the total peeled tuber. The differences may also be due to substantially different

laboratory methods used for the fiber analyses of the tubers. Schoeninger et al. 2001 used a stomacher to separate edible from inedible portions and removed the inedible portion manually before analysis (per Marlett 1992). Soluble fiber was determined by quantifying the amount of uronic acid in the contents of the stomacher using a calorimetric assay; insoluble fiber was not measured due to insufficient sample. The current study uses the NDF method, which was also used in one analysis by Vincent 1984, 1985. The NDF method measures all of the insoluble fibers but does not measure soluble fiber. In a second analysis by Vincent 1984, 1985 the crude fiber method was used, which is an antiquated method that is inaccurate for measuring fiber content (Van Soest 1994). The fact that different analytical methods have been used makes it somewhat difficult to directly compare the values presented in this analysis with previous findings. Nevertheless, the wide range of energy values for all tuber species is consistent with previous reports.

The data on baobab fruit presented in this analysis is largely consistent with previous reports (Addy & Eteshola 1993: Busson 1965; Murray et al. 2001: Nour et al. 1980; Salami & Okezie) and falls within the wide range reported for the species. Differences in the reported values of baobab fruit may be linked to differences in

analytical approaches to quantifying fiber. In some cases crude fiber analysis is used (Nour et al. 1980; Salami & Okezie 1994) and in others only cellulose is reported (Busson 1965). The study that used a measure of total dietary fiber (TDF), Murray et al. 2001, has the advantage of measuring fiber directly, however fiber was not used in any of the energy calculations. Excluding all fiber from the energy calculations may account for some of the variation between results due to the small amount of kilocalories (1 - 3 kcal/gram) that may be absorbed in the human gastrointestinal tract (Bergman 1990; Bugaut 1987). In addition, the foods in question are wild species and there may be great intra-species variation from season to season or perhaps even tree to tree (Holden et al. 2006, 2008).

The analysis reported here for tafabe berries, legumes, drupes, and figs provide the first nutrient content values for these foods. They represent foods that are typically targeted by young foragers. They have characteristics that make them ideal for children and adolescents to collect; they are relatively easy to procure and the plants tend to be located close to camp. The legumes and drupes require boiling before consumption but can provide a substantial amount of energy and/or protein to the

consumer. The next chapter will explore the extent to which juvenile foragers among the Hadza can provision themselves.

Chapter 3, in part, is currently being prepared for submission for publication of the material. The dissertation author was the primary investigator and author of this paper.

IV. Juvenile Foraging

One of the most striking characteristics of human life history is a prolonged juvenile period of growth and development (Table 1) (Charnov & Berrigan 1993; Robson et al. 2006). There are two competing evolutionary hypotheses typically sought to explain lengthened periods of juvenility in humans. The first suggests that natural selection favors prolonged investment in growth and delayed reproduction because potential reduction in fertility (due to a late age at first birth) is superseded by the benefits of a long training period in which to learn difficult foraging tasks that may reduce adult mortality (Kaplan et al. 2000). The second hypothesis suggests that a long period of childhood may be a consequence of selection for longer life-spans in general (Charnov & Berrigan 1993; Leigh 2001; Pagel & Harvey 1993).

Evolutionary models of childhood

The model proposed by Kaplan and colleagues (Kaplan et al. 2000) suggests that juvenile foraging is about learning the skills necessary to be a proficient adult, rather than actual food collection (kilocalories per day). The hypothesis uses anecdotal estimates of age at net production, with possible underestimation of production, and

does not include data on juvenile activity budgets. In addition, the hypothesis is based only on demographic data from South American foraging populations, the Ache of Paraguay and the Machiguenga of Peru.

The competing model, originally proposed by Charnov and Berrigan (1993), suggests that although children may indeed learn during childhood, the lengthened stage of juvenility is a by-product of selection on longer life spans. Only recently has data on juvenile foraging among various populations from diverse ecological settings been considered.

Data on children's foraging from the island of Mer in the Torres Strait suggests that children are not necessarily less productive foragers than adults, but are in fact making optimal foraging decisions based on their skill set and small body size (Bird & Bliege-Bird 2002). Children are smaller, slower, and have a tendency to include more species in their diet composition than adults because they encounter highly ranked resources at a lower rate (Bird & Bliege-Bird 2002). These data agree with optimal foraging models, and specifically the marginal value theorem, proposed by Charnov (1976).

Data on children's foraging from the Martu of Australia (Bird & Bliege-Bird 2005) and the Mikea of Madagascar (Tucker & Young 2005) also disagree with predictions of Kaplan's model. In these environments, children tend to focus on what Kaplan refers to as adult only "extracted" foods, such as tubers and animal meat. Children in these populations appear to be making well-informed choices about which resources to target based on the best foods for their body size (Tucker & Young 2005). Taken together, these data suggest that foraging skill does not necessarily increase with age, as predicted by Kaplan's model, but is based on educated selections of the best resource choices for children; young foragers are making the best of their small situation (Bird & Bliege-Bird 2002).

Why do children forage?

Children are in a unique position of being both dependents and workers, feeding themselves and sharing their food to provision other children. Children work because it is in their best interest to cooperate with their parents and provide economic contributions (Bock 2002; Kramer 2002) and also because they may gain fitness benefits by helping related children (Turke 1988). Adult foraging is often linked with

maintenance of social status and/or reproductive strategies, whereas the foraging of children is not (Bliege Bird & Bird 2002). When children provide nutritional assistance, they are not compromising their own reproductive success to do so (Kramer 2005a). In addition, children are neither energy limited, because they may be provisioned from the surplus of food collected by adults, nor are they time limited, because there are few alternative ways for hunter-gatherer children to spend their time (Tucker & Young 2005). Although children may not be collecting the entirety of their daily requirements, any investment helps to attenuate the high costs of raising a child to nutritional independence. In environments that are conducive to juvenile allomaternal assistance, whether in the form of childcare or provisioning, the contributions that children make to the household can have positive effects (Hawkes et al. 1995; Kramer 2002, 2004, 2005).

Previous research on Hadza children's foraging

Previous research on juvenile foraging behavior among the Hadza suggests that children and adolescents above the age of five years are capable of collecting up to 50% of their daily energy requirement (Blurton Jones et al. 1989, 1994).

Estimations are based on anecdotal data (not daily returns) and use approximations of energy value, rather than chemical composition data for the actual foods in question. The current study is in a unique position to test the above prediction using comprehensive data on children's foraging returns that includes a large sample size of foragers and detailed energy values for juvenile foods.

Aim of current study

Previous research on children's foraging has largely focused on estimations of return rates (collection per hour) (Bird & Bliege Bird 2005; Bliege Bird & Bird 2002; Blurton Jones et al. 1989) or the combined foraging effort of mothers and their children (Blurton Jones et al. 1997; Hawkes et al. 1995). The current study significantly contributes to this discussion by focusing on juvenile foraging that is conducted without adult supervision. In addition, this study is the first to go beyond comparisons of age and will explore sex differences in foraging behavior. Data on daily food returns for foragers of various ages are used to determine the extent to which young foragers are able to provision themselves, thereby offsetting the cost of their own care. The current study will quantify the amount of food collected (daily

return) by children and adolescents to determine the extent to which juvenile foraging may influence cooperative breeding among the Hadza.

Methods

Data on juvenile foraging were collected in two camps, Gangidape and Siponga, over three non-sequential months during 2005 (see Figure 1 for map of research area). Data were collected in Gangidape during the late wet season from April – May and in Siponga during the late dry season from October - November. During the late wet season watering holes were abundant and targeted foods included tubers, berries, baobab, honey, small and medium sized game animals, and a large quantity of birds, primarily weaver bird nestlings (genus *Ploceus).* During the dry season the diet was composed of berries, baobab, other fruits, and small and large game animals.

Data collection procedures

Foraging returns for children and adolescents were recorded for every day that food was brought back to camp. Of the 70 total days of data collection in the

combined camps, at least one juvenile forager returned to camp with food on 64 of the days. All food brought back to camp was measured with a hanging spring scale.

Focal follows were conducted during thirteen out of camp food collection trips by young foragers ranging in age from 5 – 14 years. Time out of camp, time spent foraging, and amount of food consumed were recorded. Distance traveled was recorded using a Garmin E-Trex Legend Handheld Global Positioning System (GPS).

Energy Determination

In order to determine the energy values for all plant foods including berries, honey, tubers, baobab, and other fruits, the inedible portions of each food (seed, husk, stem, etc.) were subtracted from the wet weight. The energy value of the remaining portion was determined using the methods and energy values of Hadza foods outlined in the previous chapter. Table 5 lists the energy values (kcal/100 grams fresh weight) used for each food type. The values from this study are extrapolated from the values in the previous chapter that report kcal/100 grams dry weight. For honey, the moisture content reported in Murray et al. 2001 was used to determine energy value. The honey values are most likely an underestimation of energy because larvae is not analyzed.

The Hadza collect the honey of stinging (*Apis mellifera*) and stingless bees (*Meliponinae*), consuming the larvae of both. The energy values for the small game meat (e.g. birds and rodents) were calculated on an individual basis for each species using published values (Table 5). In three out of four cases, no data on the chemical composition of the particular animal in question exist. In only one case, the mouse, is the genus the same; the species is different. Composition values for related species were used in all four cases.

Kin affiliation was determined by interviewing individuals in both camps and corroborating the data with long-term census data collected by Nicholas Blurton Jones (from 1982 – 1994) and Frank Marlowe (from 1995 – present). The age of the majority of juveniles in camp could be determined using the above census data that includes reproductive histories and kin affiliation of all members residing in both camps. For the few very young children that did not appear in the census data, ages were estimated based on the length of time between a woman's last recorded interview (Marlowe's census) and the current study.

Table 5: Energy values of food collected by Hadza juvenile foragers

Hadza name (English name) *Genus species*	Energy kcal/100 grams fresh weight	Reference
N//obabe (Baobab) *Adasonia digitata*	122	This study
Kongolubi (Berry) *Grewia bicolor*	244	Murray et al.(2001)
Mashalobe (Drupe) unknown *Genus species*	99	This study
Ogoyako (Fig) *Ficus sycomorus*	251	This study
Ba'alako (Honey) *Apis unicolor adansonii*	368	Murray et al. (2001)
Mangwala (Legume) *Acacia nilotica*	34	This study
//Ekwa (Tuber) *Vigna frutescens*	84	This study
Eastern Yellow Billed Hornbill (Bird)[1] *Tockus flavirostris*	158	USDA 2008
Tsoma (Weaver Bird)[1] genus *Ploceus*	158	USDA 2008
Doloka (Mouse)[2] *Acomys spinosissimus*	133	Clum et al. 1997/Prange et al. 1979
Asakala (Serval)[3] *Leptailurus serval*	120	USDA 2008

[1] No published chemical composition values were found for Weaver Birds or Eastern Yellow Hornbills. The energy value listed is extrapolated from the USDA value for guinea hens.
[2] The chemical composition data in Clum et al. 1997 os fpr the "whole body" of the mouse and does not account for the skeleton. The percent body weight was calculated from Prange et al. 1979 and then subtracted from the value published in Clum et al.
[3] No published chemical composition values were found for Serval cats. The energy value listed is extrapolated from the USDA value for a mammal of similar body size - the ground squirrel.

Statistical Analyses

The programming language R was used for all statistical analyses. For all comparisons between age and foraging return, the foragers were divided into four age groups: children in group 1 (1 – 4 years) and group 2 (5 – 9 years), and adolescents in group 3 (10 – 13 years) and group 4 (14 – 17 years). The food returns data were analyzed using a Wilcoxon rank sum test in two ways: (1) the foraging returns for each age group *per foraging trip* were compared and (2) the total foraging returns for each individual child in each age group *over all foraging trips* were compared. In order to determine if age affects the type of food collected by young foragers, a Pearson's chi square test, as a contingency table, was used. For analyses comparing the effect that sex has on foraging return, the data were analyzed using a Wilcoxon rank sum test in two ways: (1) the foraging returns for males and females *per foraging trip* were compared and (2) the total foraging returns for each individual male or female child *over all foraging trips* were compared. A Pearson's chi square test was used to determine if sex and/or age affected the type of food collected. When analyzing the focal follows data, a Wilcoxon rank sum test was used to test whether or not age and sex affected distance traveled or amount consumed while out of camp.

Statistical results of age and sex differences are graphically depicted as box plots, also known as "box-and-whisker plots (Tukey 1977). Box plots are a useful non-parametric way to represent the upper, median, and lower quartiles and outlier values of groups of numerical data. The box contains the center 50% of the data, the lower edge of the box represents the lower quartile (25^{th} percentile) and the upper edge represents the upper quartile (75^{th} percentile). The median line within the box represents the median value of the data set; if the line is not equidistant from the outside parameters of the box, the data is skewed. The horizontal lines extending from one or both sides of the box represent the interquartile range. These "whiskers" begin and end at observed data points and represent one standard deviation above and below the mean of the data. When no whiskers are depicted, the sample size is small. The data points that extend beyond the whiskers represent the outliers. Outliers are numerically distant from the rest of the data set; a high number of outliers suggest that the data has a high level of kurtosis, which means more of the variance in the data is due to extreme deviations (Tukey 1977).

Results

Wet Season Food Returns - Gangidape

A total of 19 individuals (n_1 =10 males, n_2 = 9 females) ranging in age from 1 – 17 years resided in the wet season camp, Gangidape. The study sample included a total of 14 juveniles (n_1 = 6 males, n_2 = 8 females) ranging in age from 5 – 17 years who foraged at least once. One female child, aged 7 years, had very poor eyesight, was developmentally delayed, and did not forage during our study period. Every time other children left camp on a foraging trip, she remained in camp under the care of her elderly grandfather.

Food was brought back to camp a total of 220 times. Of the total food collected during the wet season (Figure 9), the majority was from birds, with a relatively equal amount coming from tubers, honey (Ba'alako – honey from African killer bees - *Apis mellifera*), berries, and baobab.

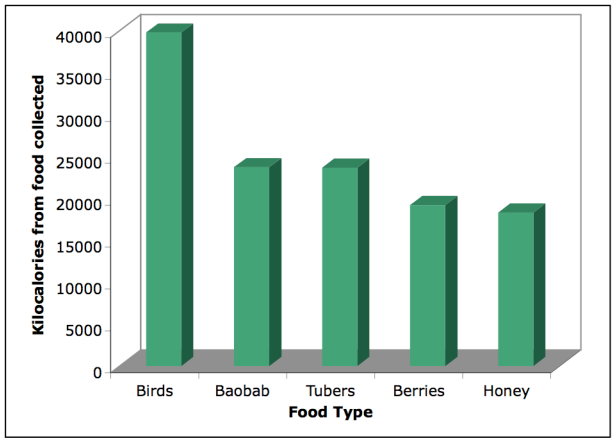

Figure 9: Wet season kilocalories from food collected

Age effects

The foragers were divided into four age groups, children: group 1 (1 – 4 years, n_1= 0 boys, n_2= 0 girls) and group 2 (5 – 9 years, n_1= 0 boys, n_2= 7 girls), and adolescents: group 3 (10 – 13 years, n_1= 4 boys, n_2= 1 girl) and group 4 (14 – 17 years, n_1= 2 boys, n_2= 0 girls). In order to determine whether age affects foraging returns, the data was analyzed in two ways. First, the mean values of amounts of food returning to camp for each age group *per foraging trip* were compared. The mean values for each age group per foraging trip (Figure 10) are as follows: group 1 = 0 kcal, group 2 = 186 kcal, group 3 = 370 kcal, and group 4 = 311 kcal. The sample size for age group 1 was zero, therefore this category was not considered in any of the age comparisons.

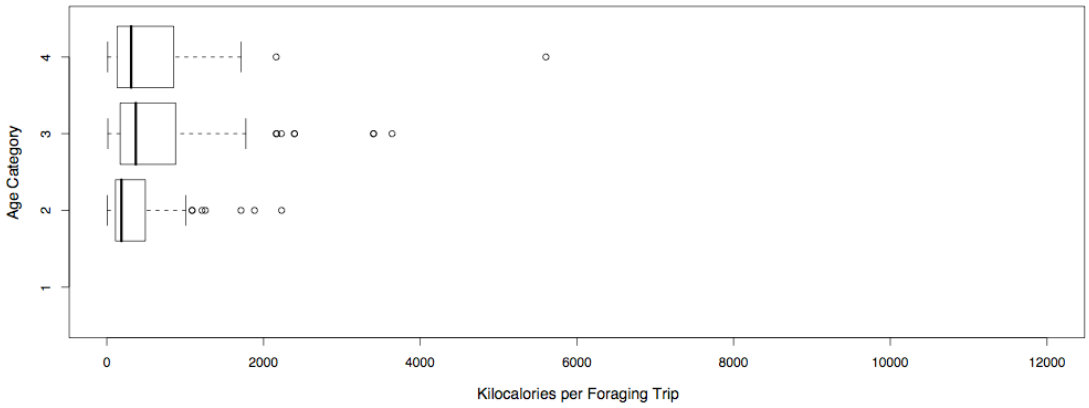

Figure 10: Total returns per foraging trip by age category – wet season

A Wilcoxon rank sum test with continuity correction was used for the following tests: age categories 2 & 3:(Wilcoxon rank sum $p < .005$, $n_1 = 85$ forays for age group 2, $n_2 = 94$ forays for age group 3), age categories 3 & 4: (Wilcoxon rank sum $p = .390$, $n_1 = 94$ forays for age group 3, $n_2 = 41$ forays for group 4), and age categories 2 & 4: (Wilcoxon rank sum $p = .063$, $n_1 = 94$ forays for age group 2, $n_2 = 41$ forays for group 4). In the comparison between age groups 2 and 3, older children (age group 3) bring back significantly more kilocalories than younger children (age group 2). In addition, when comparing age groups 2 and 4, older children (age group 4) bring back more kilocalories than their younger counterparts (age group 2), although the difference is

not quite significant. When comparing age categories 3 and 4, age is not a significant predictor of how much food is brought back to camp.

The second analysis was a comparison between the mean values of *total food* brought back to camp by each individual in each age group *over all foraging trips combined.* Mean overall individual food collection returns for each age group across all foraging trips (Figure 11) are as follows: group 1= 0 kcal, group 2 = 900 kcal, group 3 = 13,234 kcal, and group 4 = 13,722 kcal. Again, due to the sample size of 0, age category 1 was not considered in any of the following comparisons.

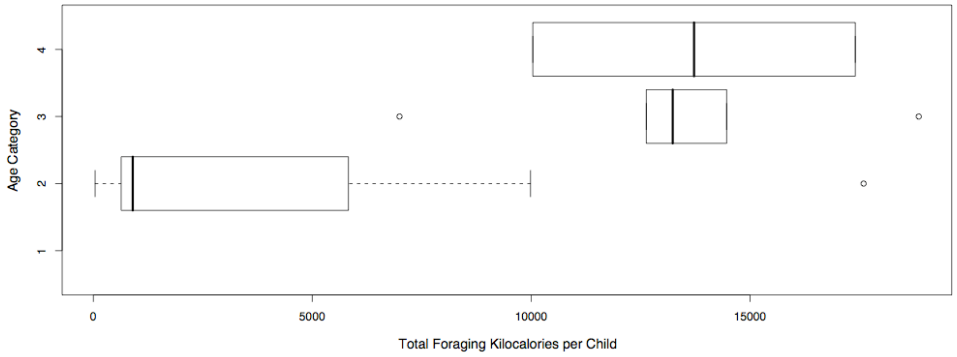

Figure 11: Total individual returns over all foraging trips by age category – wet season

A Wilcoxon rank sum test was used for the following tests: age categories 2 & 3: (Wilcoxon rank sum p = .05, n_1 = 7 children for age group 2, n_2 = 5 adolescents for age group 3), age categories 3 & 4: (Wilcoxon rank sum p = 1, n_1 = 5 adolescents for

age group 3, $n_2 = 2$ adolescents for age group 4), age categories 2 & 4: (Wilcoxon rank sum p = .222, $n_1 = 7$ children for age group 2, $n_2 = 2$ adolescents for age group 4). Age groups 3 and 4 have greater overall collection returns when compared to age group 2, however the differences are not quite significant.

Age is a strong predictor of food type collected (chi squared = 75.4, df = 10, p < .001). Figure 12 depicts the frequency of food type returning to camp, split by age group. Children in age group 2 (5 – 9 years) tend to collect berries the most frequently, then decreasingly on tubers, baobab, and birds. Adolescents in age group 3 (10 – 13 years) most frequently collect birds, then decreasingly on baobab, berries, honey, and tubers. Adolescents in age group 4 (14 – 17 years) most frequently target birds, followed decreasingly by baobab, tubers, and honey.

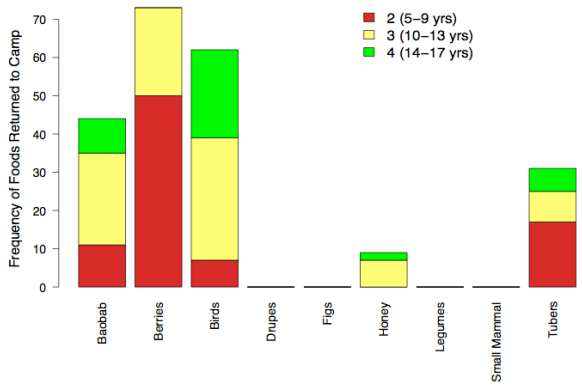

Figure 12: Frequency of food type collected, split by age – wet season

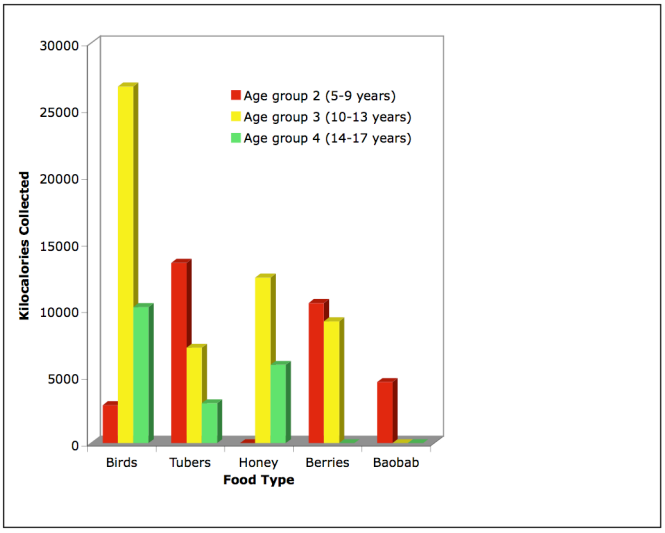

Figure 13: Total kilocalories from food collected, split by age – wet season

The food type most frequently collected is not necessarily the food type that contributes the most kilocalories during wet season collection. Figure 13 depicts the total wet season kilocalories collected, split by age group. The foods providing the most energy for children in age group 2 (5 – 9 years) are tubers, followed by berries, baobab, and birds. For children in age group 3 (10 – 13 years) and age group 4 (14 – 17 years), the food types contributing the most energy (Figure 13) are also the food types most frequently collected (Figure 12).

Sex effects

In order to determine if sex has an effect on foraging return, the data was again analyzed in two different ways. The mean values of the amounts of food returning to camp for both males and females *per foraging trip* were compared. The mean returns per trip are 403 kcal for males (n = 10 individuals) and 206 kcal for females (n = 9 individuals) (Figure 14). Sex has a significant effect on the amount of food brought back to camp on a given foraging trip (Wilxocon rank sum p = .003, n_1 = 104 forays for males, n_2 = 116 forays for females); per foray, male foragers bring back more kilocalories to camp.

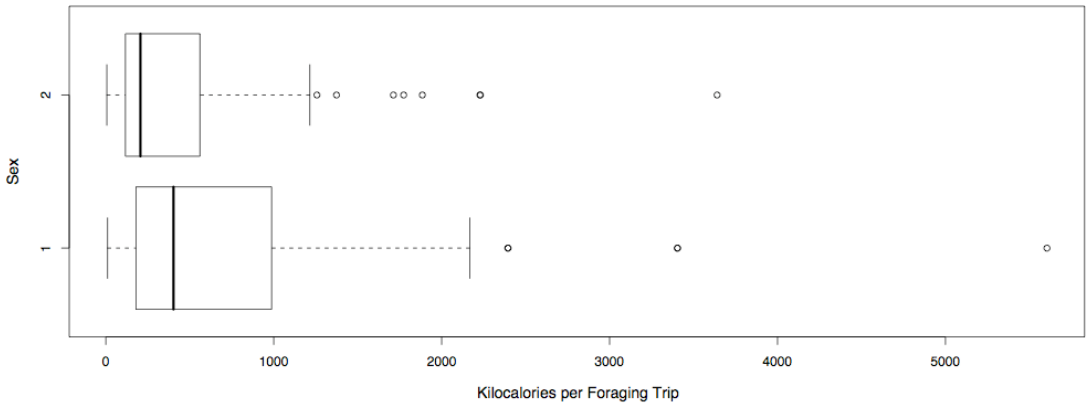

Figure 14: Total returns per foraging trip by sex – wet season (1 = male, 2 = female)

When comparing overall individual mean returns for males and females across *all foraging trips*, the mean value for males is 12,932 kcal (n = 10 individuals) and

1283 kcal for females (n = 9 individuals) (Figure 15). Male foragers appear to bring back more kilocalories to camp, although it is not a significant difference (Wilcoxon rank sum p = .181, n_1 = 10 males, n_2 = 9 females), which is most likely due to small sample size.

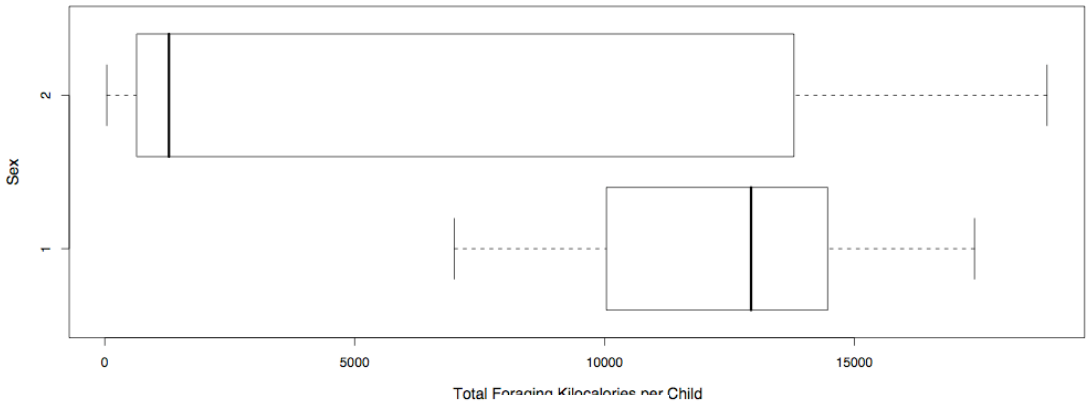

Figure 15: Total individual returns over all foraging trips by sex– wet season (1 = male, 2 = female)

In terms of frequency and overall energy contribution, male foragers tend to focus primarily on birds and baobab (Figures 16 and 17). Female foragers most frequently collect berries, followed decreasingly by tubers, baobab, and birds (Figure 16). The most kilocalories collected overall, however, are provided from tubers, and then decreasingly from berries, birds, and baobab (Figure 17).

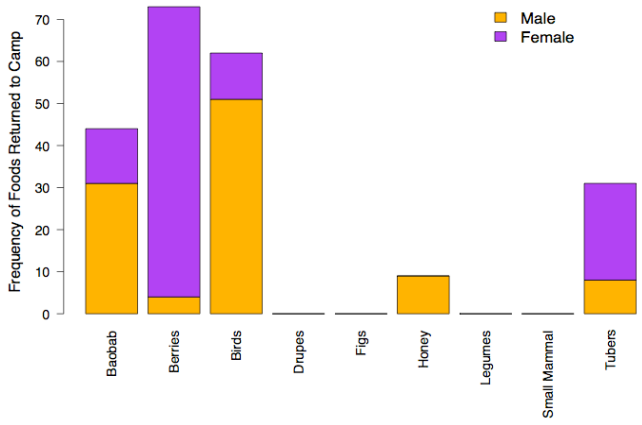

Figure 16: Frequency of food type collected, split by sex – wet season

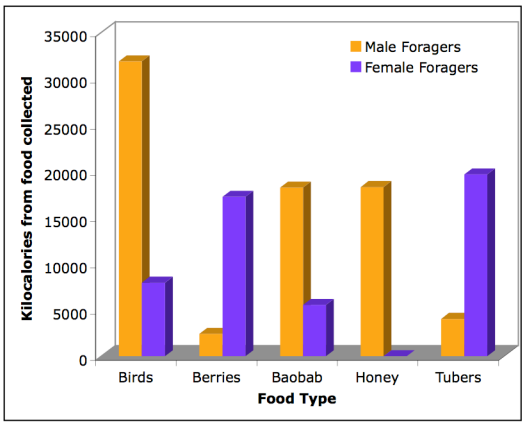

Figure 17: Total kilocalories collected from food, split by sex – wet season

Dry Season Food Returns

A total of 24 individuals ($n_1 = 9$ males, $n_2 = 15$ females) ranging in age from 1 – 17 years resided in the dry season camp, Siponga. The study sample included a total

of 20 juveniles (n_1 = 8 males, n_2 = 12 females) ranging in age from 3 – 17 years who foraged at least once.

Food was brought back to camp a total of 261 times. Of the total food young foragers brought into camp during the dry season (Figure 18), the majority is from fruit. Figs are collected the most, followed by baobab, both of which are supplemented with relatively equal amounts of small mammals, birds, drupes, and berries. A small amount of legumes are also collected.

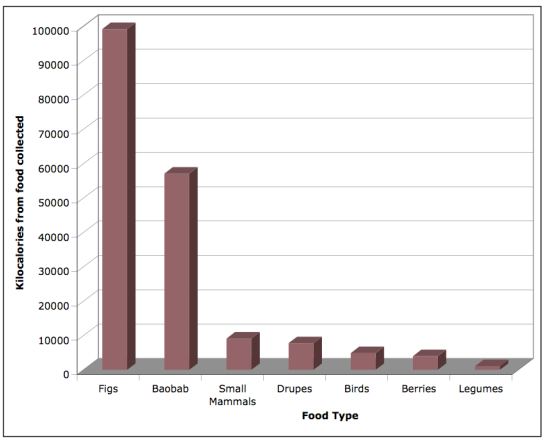

Figure 18: Dry season kilocalories from food collected

Age effects

The foragers were divided into four age groups, children: group 1 (1 – 4 years, n_1= 1 boy, n_2= 0 girls) and group 2 (5 – 9 years, n_1= 3 boys, n_2= 6 girls), and

adolescents: group 3 (10 – 13 years, n_1= 4 boys, n_2= 1 girl) and group 4 (14 – 17 years, n_1= 0 boys, n_2= 5 girls). The mean values for each age group per foraging trip (Figure 19) are as follows: group 1 = 325 kcal, group 2 = 420 kcal, group 3 = 140 kcal, and group 4 = 307 kcals. The sample size for age group 1 is one individual, therefore this category was not considered in any of the age comparisons.

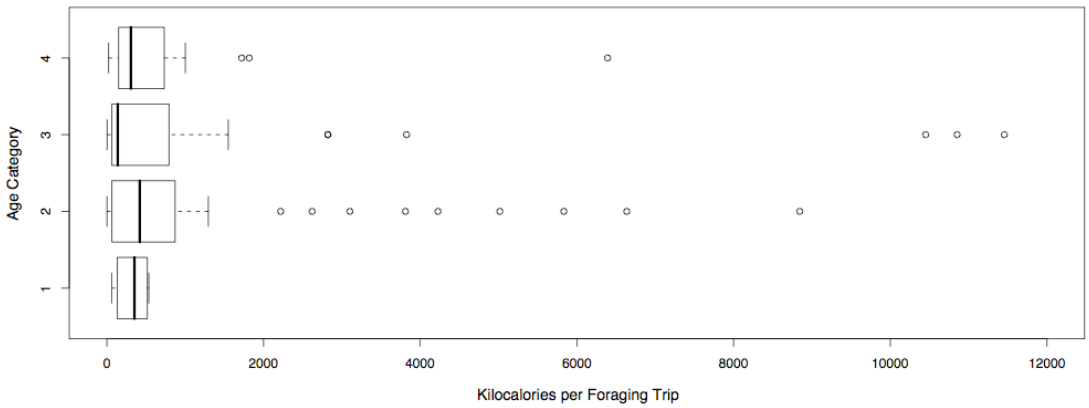

Figure 19: Total returns per foraging trip by age category – dry season

A Wilcoxon rank sum test with continuity correction was used for the following tests: age categories 2 & 3:(Wilcoxon rank sum p = .387, n_1 = 114 forays for age group 2, n_2 = 97 forays for age group 3), age categories 3 & 4: (Wilcoxon rank sum p = .179, n_1 = 97 forays for age group 3, n_2 = 47 forays for group 4), and age categories 2 & 4: (Wilcoxon rank sum p = .772, n_1 = 114 forays for age group 2, n_2 =

47 forays for group 4). In each comparison, age is not a significant predictor of how much food is brought back to camp.

The second analysis was a comparison between the mean values of *total food* brought back to camp by each individual in each age group *over all foraging trips combined.* Mean overall individual food collection returns for each age group across all foraging trips (Figure 20) are as follows: group 1= 325 kcal, group 2 = 4866 kcal, group 3 = 2898 kcal, and group 4 = 4139 kcal. Again, due to the small sample size of age category 1, it was not considered in any of the following comparisons.

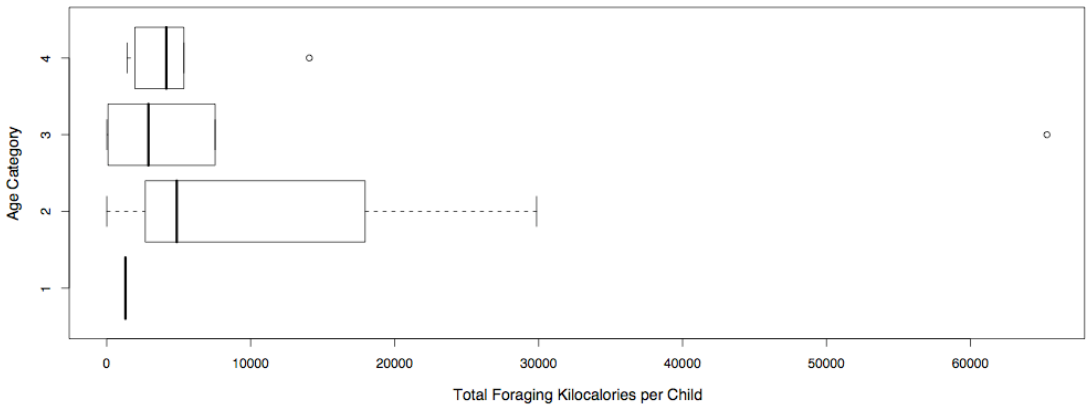

Figure 20: Total individual returns over all foraging trips by age category – dry season

A Wilcoxon rank sum test was used for the following tests: age categories 2 & 3: (Wilcoxon rank sum p = .899, n_1 = 9 children for age group 2, n_2 = 5 adolescents for

age group 3), age categories 3 & 4: (Wilcoxon rank sum p = .841, n_1 = 5 adolescents for age group 3, n_2 = 5 adolescents for age group 4), age categories 2 & 4: (Wilcoxon rank sum p = .699, n_1 = 9 children for age group 2, n_2 = 5 adolescents for age group 4). In each comparison age is not a significant predictor of how much food is brought back to camp.

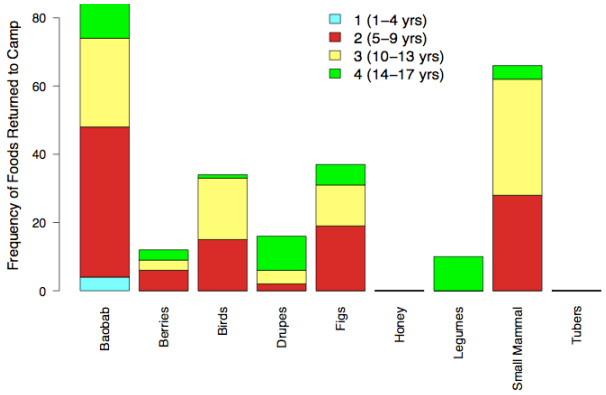

Figure 21: Frequency of food type collected, split by age – dry season

Age is a strong predictor of the type of food collected (chi squared = 106.6, df = 24, p < .001). Figure 21 depicts the frequency of food type collected, split by age. The child in age group 1 (1-4 years) focused only on baobab fruit. Children in age group 2 (5 – 9 years) most frequently collect baobab, and then small mammals, figs, birds, and berries in decreasing frequency. Adolescents in age group 3 (10 – 13 years)

most frequently collect small mammals and baobab, followed by birds, figs, drupes, and berries. Adolescents in age group 4 (14 – 17 years) most frequently collect legumes, drupes, and baobab (with relatively equal frequency), followed by figs, berries, small mammals and birds; these foods are also the foods that contribute the most energy to the collection yield of children in age group 4 (Figure 22).

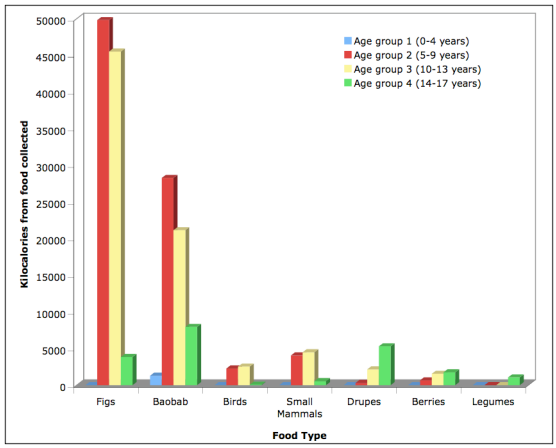

Figure 22: Total kilocalories from food collected, split by age – dry season

For children in age groups 2 (5 – 9 years) and 3 (10 – 13 years), the overall amount of kilocalories provided by food type does not correspond with the frequency in which specific food types are collected. They most frequently collect baobab and small mammals, however figs and baobab are the foods that provide the bulk of their energy (Figure 22).

Sex effects

In order to determine if sex has an effect on foraging return, the data was again analyzed in two different ways. The mean values of the amounts of food returning to camp for both males and females *per foraging trip* were compared. The mean returns per trip are 77 kcal for males (n = 8 individuals) and 599 kcal for females (n = 12 individuals) (Figure 23). Sex has a significant effect on the amount of food brought

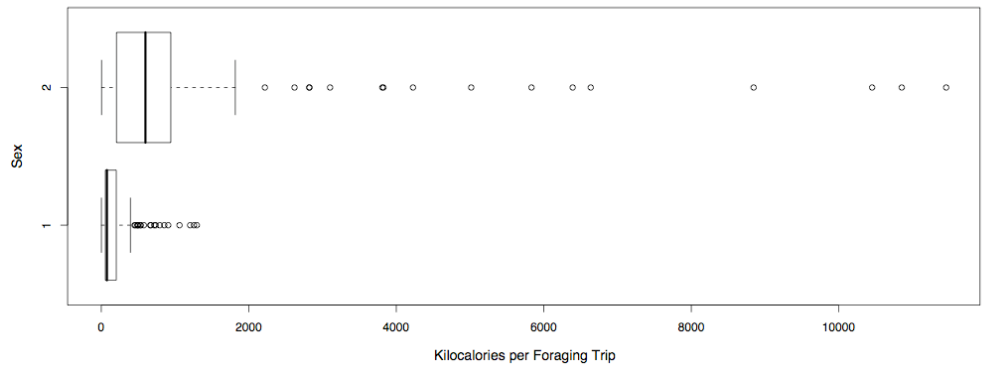

Figure 23: Total returns per foraging trip by sex – dry season (1 = male, 2 = female)

back to camp on a given foraging trip (Wilcoxon rank sum $p < .005$, $n_1 = 111$ forays for males, $n_2 = 151$ forays for females); girls bring back more kilocalories to camp. When comparing mean overall returns for males and females across *all foraging trips*, the mean value for males is 1988 kcal (n = 8 individuals) and 5112 kcal for females (n = 12 individuals) (Figure 24). Although girls tend to bring back more kilocalories,

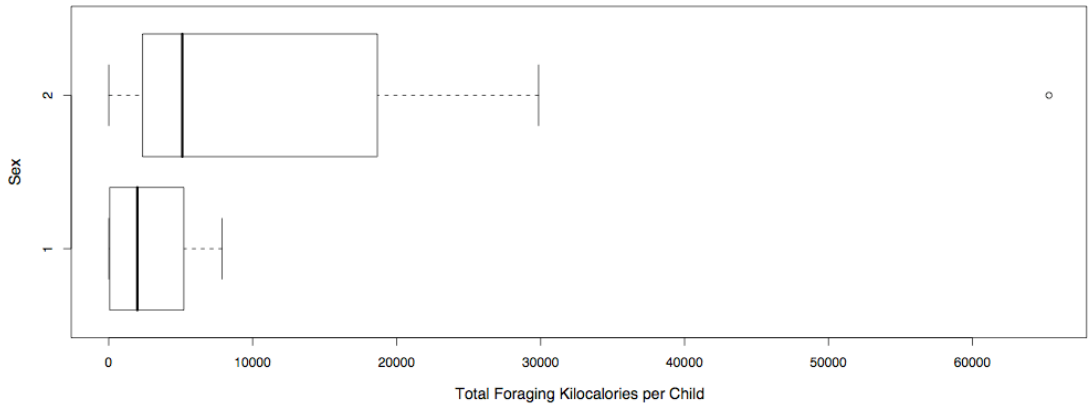

Figure 24: Total individual returns over all foraging trips by sex– dry season (1= male, 2 = female)

sex has no significant effect on the overall amount of food brought back to camp (Wilcoxon rank sum p = .082, n_1 = 8 males, n_2 = 12 females). In terms of foods targeted, however, there is a significant difference between the foods brought back to camp by males versus those brought back to camp by females (chi squared = 151.67, df = 8, p < .001). Young male foragers most frequently collect small mammals and birds followed by baobab (Figure 25). Young female foragers, however, most frequently collect baobab and then decreasingly focus on figs, drupes, berries, and legumes (Figure 25).

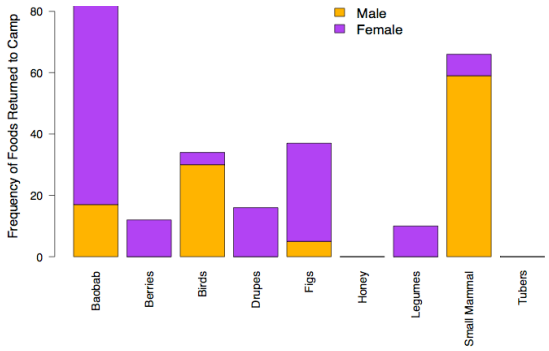

Figure 25: Frequency of food type collected, split by sex – dry season

During the dry season, the foods providing the bulk of the energy collected are similar to those that are collected most frequently, with one notable exception; although figs are not targeted the most frequently by young female foragers, they provide the greatest amount of energy (Figure 26).

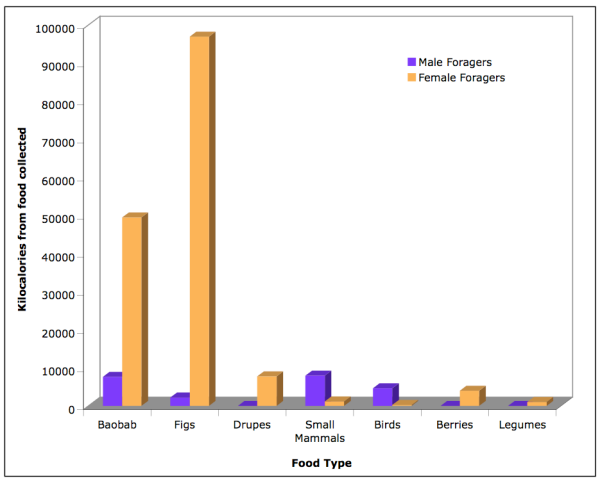

Figure 26: Total kilocalories from food collected, split by sex – dry season

Wet Season vs. Dry Season

In order to determine if season is affecting the age related differences in returns, a Wilcoxon rank sum test with continuity correction was used to compare each age group during the wet and dry season. For children in age group 2 (5 – 9 years), seasonality has no significant effect on overall return (Wilcoxon rank sum p = .362, n1 = 85 forays for wet season, and n2= 114 forays for dry season). For adolescents in age group 4 (14 – 17 years), seasonality also has no effect on overall return (Wilcoxon rank sum p = .747, n1 = 41 forays for wet season, and n2= 47 forays for dry season). Young foragers in age group 3 (10 -13 years), however, collect significantly more kilocalories during the wet season than the dry season (Wilcoxon rank sum p = .001, n1 = 94 forays for wet season, and n2= 97 forays for dry season).

To determine if season affects sex related differences in food collection, a Wilcoxon rank sum test with continuity correction was used to compare male foraging return during the wet and dry season and female foraging return during the wet and dry season. Season has a significant effect on male and female foraging. During the rainy season the mean collection of male foragers is 403 kcal, which is significantly higher than their mean collection during the dry season, which is 77 kcal (Wilcoxon rank sum $p < .005$, $n_1 = 403$ cases of food collection for wet season, $n_2 = 111$ cases of

food collection for the dry season). Conversely, female foragers collect significantly more during the dry season than during the wet season (Wilcoxon rank sum $p < .005$, , $n_1 = 116$ cases of food collection for wet season, $n_2 = 151$ cases of food collection for the dry season); the mean collection of young female foragers during the wet season is 206 kcal, versus 599 kcal during the dry season.

Overall Food Returns – Wet season and dry season pooled

A total of 43 individuals ($n_1 = 18$ males, $n_2 = 25$ females) ranging in age from 1 – 17 years resided in the camps reported in this study. The study sample included a total of 34 juveniles ($n_1 = 14$ males, $n_2 = 20$ females) ranging in age from 3 – 17 years who foraged at least once.

Food was brought back to camp a total of 483 times. Of the total kilocalories young foragers brought into camp across both seasons (Figure 27), the majority was from fruit (figs, baobab, drupes, and berries), with a relatively equal amount coming from tubers and honey, and supplemented with small mammals and legumes.

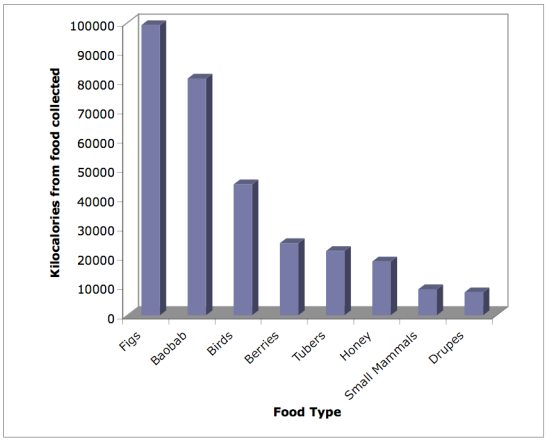

Figure 27: Total kilocalories from food collected

Age effects

The foragers were divided into four age groups, children: group 1 (1 – 4 years, n_1= 1 boy, n_2= 0 girls) and group 2 (5 – 9 years, n_1= 3 boys, n_2= 13 girls), and adolescents: group 3 (10 – 13 years, n_1= 8 boys, n_2= 2 girls) and group 4 (14 – 17 years, n_1= 2 boys, n_2= 5 girls). The mean values for each age group per foraging trip (Figure 28) are as follows: group 1 = 325 kcal, group 2 = 225 kcal, group 3 = 333 kcal, and group 4 = 310 kcals. The sample size for age group 1 was 1 individual, therefore this category was not considered in any of the age comparisons.

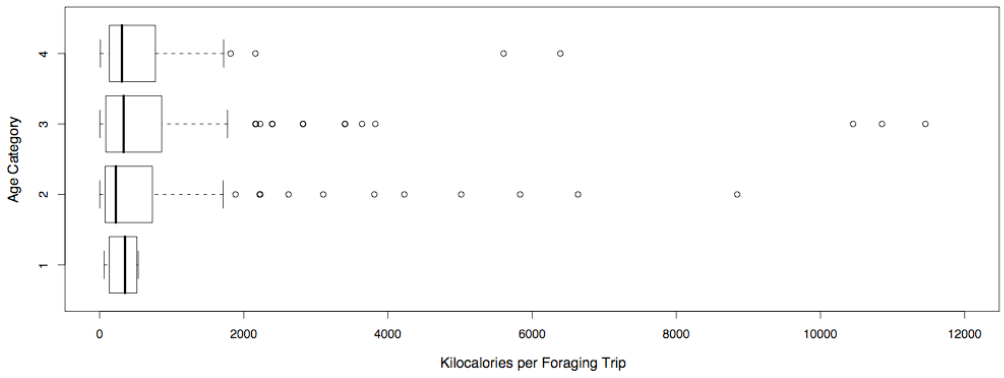

Figure 28: Total returns per foraging trip by age category – across seasons

A Wilcoxon rank sum test with continuity correction was used for the following tests: age categories 2 & 3:(Wilcoxon rank sum p = .152, n_1 = 199 forays for age group 2, n_2 = 191 forays for age group 3), age categories 3 & 4: (Wilcoxon rank sum p = .847, n_1 = 191 forays for age group 3, n_2 = 88 forays for group 4), and age categories 2 & 4: (Wilcoxon rank sum p = .143, n_1 = 199 forays for age group 2, n_2 = 88 forays for group 4). In each comparison, age was not a significant predictor of how much food was brought back to camp.

The second analysis was a comparison between the mean values of *total food* brought back to camp by each individual in each age group *over all foraging trips combined.* Mean overall individual food collection returns for each age group across all foraging trips (Figure 29) are as follows: group 1= 325 kcal, group 2 = 2708 kcal,

group 3 = 10,081 kcal, and group 4 = 5357 kcal. Again, due to the small sample size of age category 1, it was not considered in any of the following comparisons.

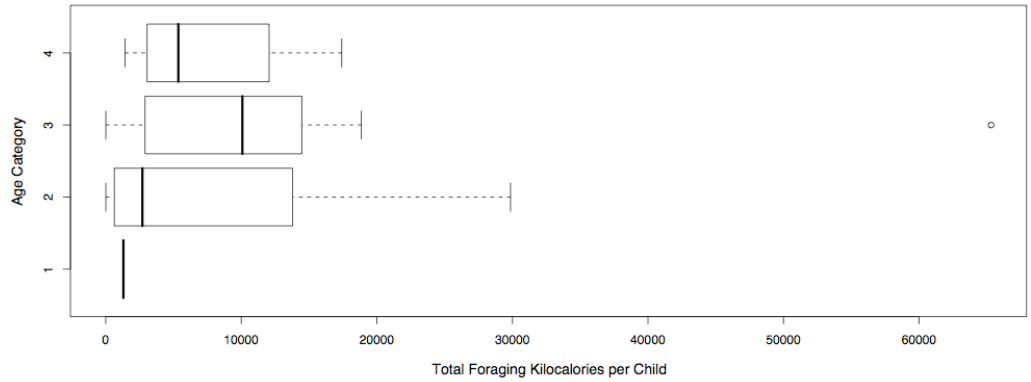

Figure 29: Total individual returns over all foraging trips by age category – across seasons

A Wilcoxon rank sum test was used for the following tests: age categories 2 & 3: (Wilcoxon rank sum p = .336, n_1 = 16 children for age group 2, n_2 = 10 adolescents for age group 3), age categories 3 & 4: (Wilcoxon rank sum p = .669, n_1 = 10 adolescents for age group 3, n_2 = 7 adolescents for age group 4), age categories 2 & 4: (Wilcoxon rank sum p = .451, n_1 = 16 children for age group 2, n_2 = 7 adolescents for age group 4). In each comparison age was not a significant predictor of how much food was brought back to camp.

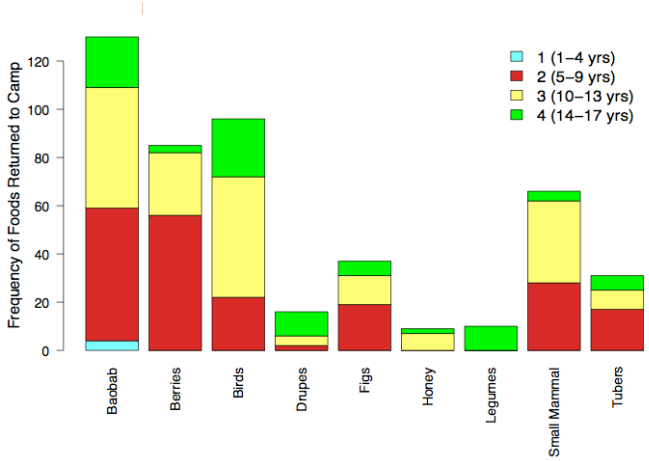

Figure 30: Frequency of food type collected, split by age – across seasons

Age is a strong predictor of the type of food collected (chi squared = 82.87, df = 15, $p < .001$). The child in age group 1 (1-4 years) focused only on baobab fruit. Children in age group 2 (5 – 9 years) most frequently collect baobab and berries, followed by small mammals, birds, figs, and tubers (Figure 30). Figs, although not collected the most frequently, have the greatest energetic contribution, followed by baobab, tubers, and berries (Figure 31). Adolescents in age group 3 (10 – 13 years) most frequently collect birds and baobab, followed decreasingly by small mammals, berries, and figs (Figure 30). For this age group, figs also provide the greatest energetic contribution even though they are not targeted with the highest frequency;

baobab and small mammals also provide substantial amounts of energy (Figure 31). Adolescents in age group 4 (14 – 17 years) most frequently target birds and baobab (in relatively equal amounts) followed by drupes and legumes (Figure 30); birds and baobab also provide the most energy for adolescents in this age group (Figure 31).

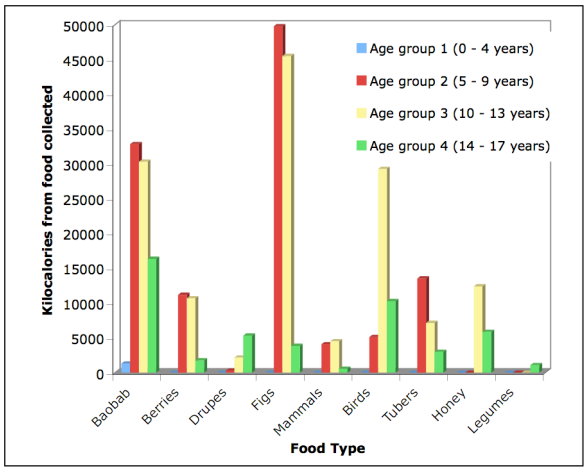

Figure 31: Total kilocalories from food collected, split by age – across seasons

Sex effects

In order to determine if sex has an effect on foraging return, the data was again analyzed in two different ways. The mean values of the amounts of food returning to camp for both males and females *per foraging trip* were compared. The mean returns

per trip are 171 kcal for males (n = 14 individuals) and 430 kcal for females (n = 20 individuals) (Figure 32). Sex has a significant effect on the amount of food brought to camp on a given foraging trip (Wilcoxon rank sum $p < .005$, $n_1 = 215$ forays for males, $n_2 = 267$ forays for females); girls bring back more kilocalories to camp.

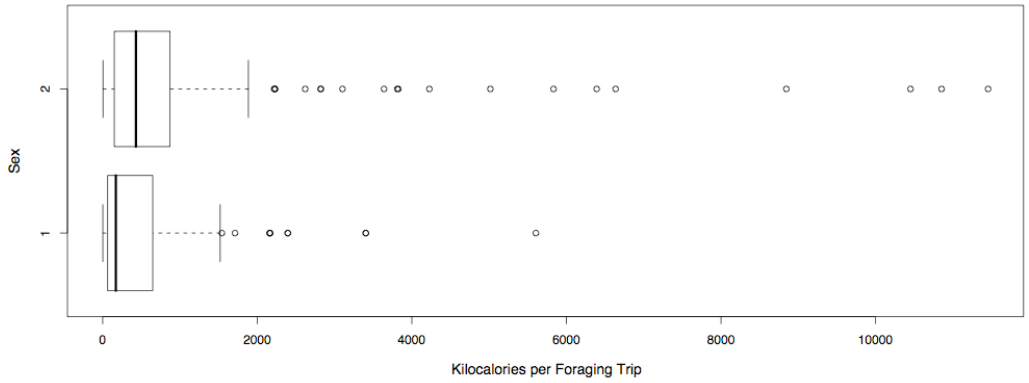

Figure 32: Total returns per foraging trip by sex – across seasons (1 = male, 2 = female)

When comparing mean overall returns for males and females across *all foraging trips*, the mean value for males is 7263 kcal (n = 14 individuals) and 4501 kcal for females (n = 20 individuals) (Figure 33). Although girls tend to bring back more kilocalories, sex has no significant effect on the overall amount of food brought back to camp (Wilcoxon rank sum $p = .717$, $n_1 = 14$ males, $n_2 = 20$ females).

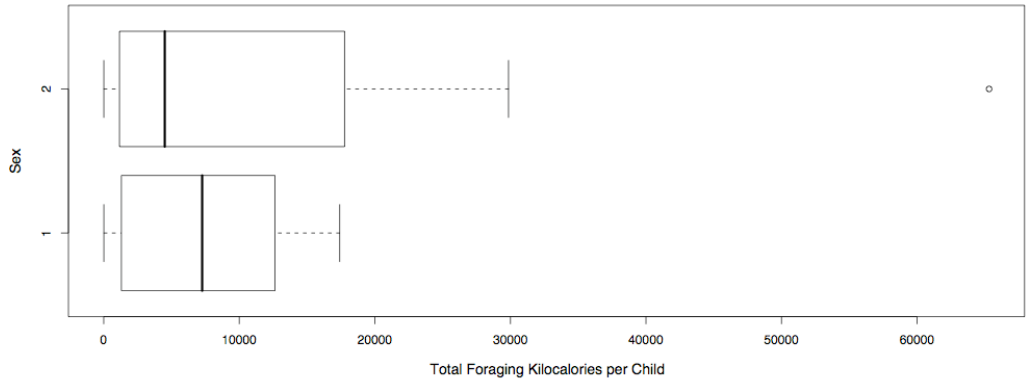

Figure 33: Total individual returns over all foraging trips by sex– across seasons (1= male, 2 = female)

In terms of foods targeted, however, there is a significant difference between the foods brought back to camp by males versus those brought back to camp by females (chi squared =208.101, df = 7, $p < .001$). Young male foragers most frequently collect, in decreasing order, birds, small mammals, and baobab (Figure34). The foods making the largest energetic contribution to the foraging returns of male foragers, in decreasing order, are birds, baobab, honey, small mammals, and tubers (Figure 35). Young female foragers collect baobab and berries the most frequently and then, with decreasing frequency, collect figs, tubers, drupes, berries, and legumes

(Figure 34). The foods which contribute the most energy to the collection yield of female foragers are figs, followed by baobab, tubers, berries, and drupes (Figure 35).

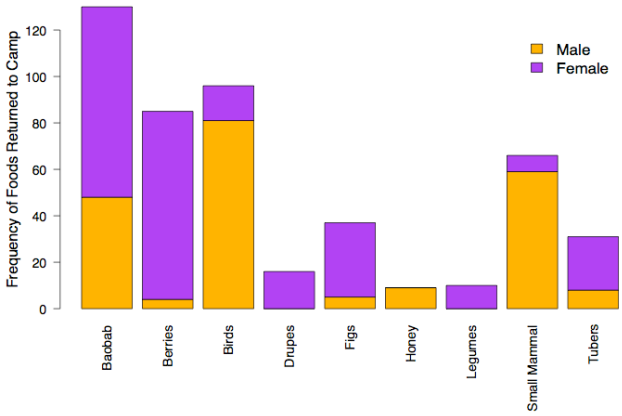

Figure 34: Frequency of food type collected, split by sex – across seasons

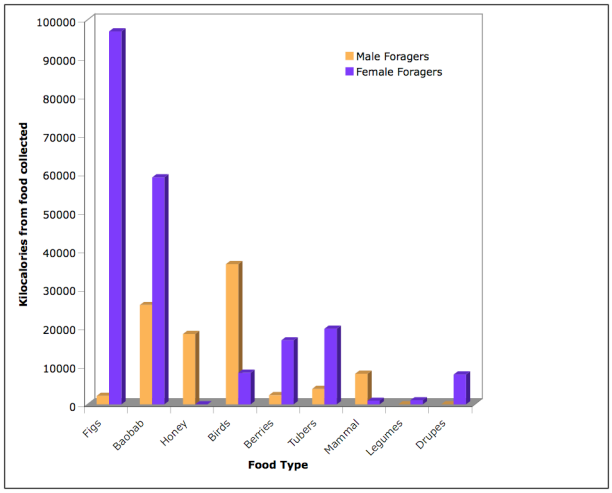

Figure 35: Total kilocalories from food collected, split by sex – across seasons

Estimated energy production

The food returns analyses can be used to estimate the degree to which children and adolescents are able to provision themselves. The age and sex specific daily energy requirements for each forager are not known, however estimates can be obtained using published values of energy requirements (Institute of Medicine of the National Academies 2002) based on the age and weight of each individual. Table 6 lists the average daily yield for each individual forager in the sample and the estimated range of daily energy needs, which is based on a variation of $\pm$ 400 kilocalories at any given age and variation in work-load (Garrow 1978). If the lower range of daily energy requirements is used as the estimate, the average daily collections of 9 individuals meet 25%-40% of their daily needs; 5 individuals meet 41-75%; and 1 individual exceeds 90%. Foragers numbered 19 and 21 represent the only two individuals whose average daily collection approximately meets or exceeds the lower range of daily energy requirements.

Table 6: Average Daily Returns for Individual Foragers

Category	**Individual Forager**	**Age** (years)	**Sex** 1= male 2 = female	**Average Daily Production (kcal)**	**Daily Estimated Energy Requirement (kcal)*** (Range of low - high)	**Number of Days Foraged**
Wet Season - Gangidape						
Group 2	1	5	2	225	1379 - 1557	4
(5 - 9 years)	2	6	2	126	1451 - 1642	3
	3	6	2	149	1451 - 1642	6
	4	6	2	40	1451 - 1642	1
	5	8	2	151	1593 - 1810	11
	6	9	2	312	1660 - 1890	31
	7	9	2	628	1660 - 1890	28
Group 3	8	10	1	1263	1875 - 2149	10
(10 - 13 years)	9	10	1	575	1875 - 2149	23
	10	10	2	608	1729 - 1972	31
	11	11	1	538	1985 - 2279	13
	12	12	1	851	2113 - 2428	17
Group 4	13	14	1	622	2459 - 2829	28
(14 - 17 years)	14	17	1	772	2796 - 3226	13
Dry Season - Siponga						
Group 1 (1 - 4 years)	15	3	1	325	1324 - 1485	4
Group 2	16	5	2	9	1379 - 1557	1
(5 - 9 years)	17	5	2	685	1379 - 1557	4
	18	5	2	487	1379 - 1557	10
	19	6	2	1572	1451 - 1642	18
	20	6	1	669	1535 - 1742	4
	21	7	2	2564	1515 - 1719	7
	22	8	2	842	1593 - 1810	23
	23	9	1	37	1787 - 2043	1
Group 3	24	10	1	209	1875 - 2149	36
(10 - 13 years)	25	10	2	1633	1729 - 1972	40
	26	11	1	842	1985 - 2279	45
	27	12	1	11	2113 - 2428	1
	28	13	1	93	2276 - 2618	1
	29	13	1	153	2276 - 2618	19
Group 4	30	14	2	345	2036 - 2334	12
(14 - 17 years)	31	15	2	475	2057 - 2362	3
	32	16	2	392	2059 - 2368	5
	33	16	2	383	2059 - 2368	14
	34	17	2	1082	2042 - 2353	12

* Values extracted from Institute of Medicine of National Academies Press (2002). The recommended daily allowances are taken from this reference because this text estimates energy needs based on weight and sex of the child.

Focal Follows

Thirteen focal follows were conducted during out of camp foraging trips with individual foragers ranging in age from 5 – 14 years (n_1 = 7 males, n_2 = 6 females). The duration of trips ranged from 40 minutes to five hours; distance traveled ranged from 300 meters to approximately 7 kilometers (Table 7). Only two out of the total thirteen focal follows were from the dry season camp, Siponga, therefore the sample size was too small to analyze each camp independently. The following analyses use data from the combined camps.

Table 7: Focal follows of juvenile foragers

Focal Follow	Sex of Forager (1=male, 2=female)	Age of Forager (years)	Distance Traveled (kilometers)	Duration of Follow (Minutes)	Calories Consumed
1	2	6	0.6	47	94
2	2	9	0.4	42	106
3	2	10	3.5	163	301
4	2	10	1.7	144	236
5	2	10	1.5	65	1860
6	2	9	0.5	116	1986
7	2	5	1.1	69	84
8	1	10	1.6	105	3304
9	1	10	2.1	196	3082
10	1	10	0.8	75	3097
11	1	10	1.2	66	796
12	1	14	1.2	178	2275
13	1	14	6.9	315	1049

Age has an effect on distance traveled, younger children stayed closer to camp (Wilcoxon rank sum test n_1 = 4 follows of children < 10 years, n_2 = 9 follows of

children > 10 years, p = .005). Sex, however, does not have an effect on distance traveled (Wilcoxon rank sum test $n_1 = 7$ males, $n_2 = 6$ females, p = .295); the average distance was 2.3 km for males and 1.3 km for females (Figure 36). One male child was an exceptional hunter and honey collector (Table 6, forager 13) who consumed most of his collection while out of camp. He tended to travel for longer distances and is an extreme outlier. Per foraging trip, males consume significantly more than females (Wilcoxon rank sum test $n_1 = 7$ males, $n_2 = 6$ females, p = .014). Figure 37 depicts the range of consumption per trip for males (mean = 2,267 kcal) and females (mean = 667 kcal).

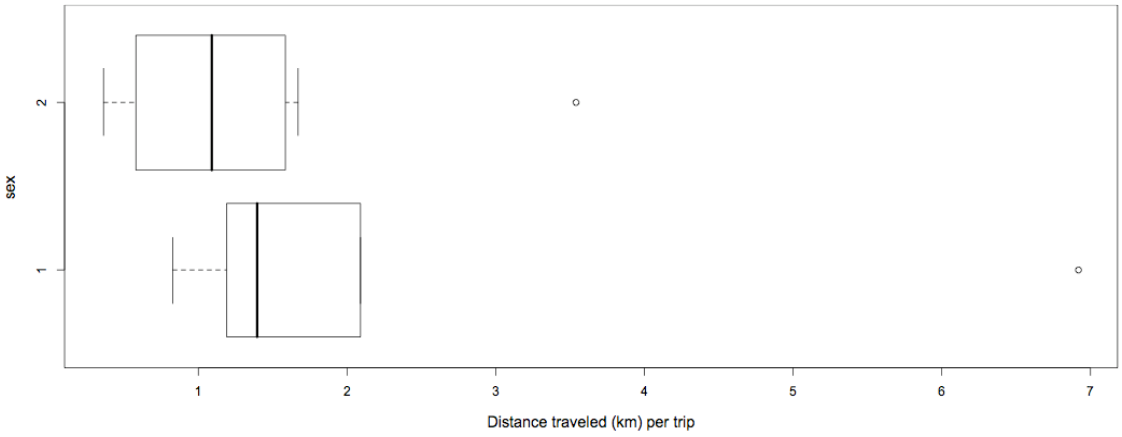

Figure 36: Distance traveled per foraging trip (kilometers) by sex (1=male, 2= female)

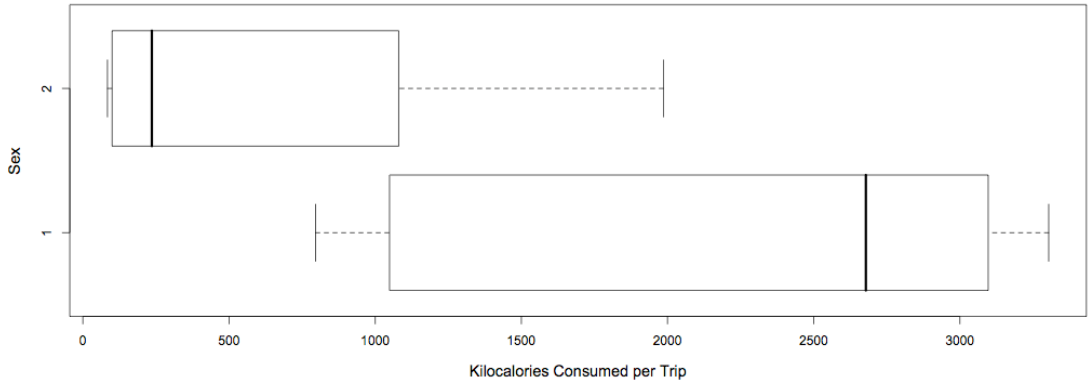

Figure 37: Kilocalories consumed per foraging trip by sex (1=male, 2=female)

Discussion

Hadza children begin routine collection of various types of foods starting at the age of five years (Figure 38). Although some foods are available year round, such as baobab, there are striking seasonal differences in foods collected. In addition, seasonal availability of foods influences sex and age differences in foods targeted and amount collected. During the wet season, food brought back to camp includes birds, baobab, tubers, berries, and honey. During the dry season, the bulk of the food returning to camp is fruit (figs and baobab) supplemented with small amounts of small mammals, birds, and legumes.

Figure 38: Children of various ages with baobab fruit

Foraging choices of children in age group 2 (ages 5 – 9 years)

Younger children (age group 2: 5 – 9 years) collect fewer kilocalories during the wet season when compared to other age groups. During the wet season, children in this age range primarily obtain their energy from tubers and berries, with a small amount coming from baobab and birds. Berries yield a significant amount of energy per 100 grams (Table 5), however obtaining a large yield of berries might be difficult for children who are not tall enough to reach the upper berry branches and have small hands and therefore collect smaller handfuls of berries. Berries are a relatively difficult food to collect because they require effort to pull from the branches, they are small in size with large seeds and a small proportion of fleshy pulp (see previous chapter), they

require secondary processing to remove twigs and leaves, and berry patches may be located somewhat far from camp. Although the collection and processing costs may be high, there are few alternate food choices with a high energy value that young children can target during the wet season. Tubers are also difficult for young children to collect because successful digging requires knowledge of where to find the underground storage organs; a skill that can be difficult to master. Young children are also unable to collect a significant amount of weaver birds during the wet season because they are shorter in stature than the other children and it may be difficult to reach the nests which can reside somewhat high in the trees.

During the dry season, children in this age range are able to collect as much as older children and typically focus their collection on figs and baobab. Baobab fruit is easy to collect and is available year round. Although it requires secondary processing to extract the pulp from the outer capsule and then subsequently pound it into powder, this food provides approximately 122 kcal/100g fresh weight (Table 5). Children are quite adept at using the large round stones to pound the pulp (Figure 39) and tend to find stones smaller than those used by adults that fit easily within their grasp.

Similarly, figs are an ideal food for young children to target because they are easy to collect, require no processing, and have a high energy value (Table 5).

Figure 39: Young female forager pounding baobab seeds

Foraging choices of adolescents in age group 3 (ages 10 - 13 years)

Adolescent foragers in age group 3 (10 – 13 years) collect significantly more kilocalories during the wet season than the dry season. The bulk of the energy provided by food is from birds and honey, followed by berries and tubers. The high percentage of birds collected during the wet season (Figure 9) can be linked to the seasonal reproduction of the weaver birds that inhabit Northern Tanzania (*Ploceus* sp.). Weaver birds are colonial breeders that commence breeding during the rainy seasons when occupying habitats close to the equator (Britton 1980; Dittami 1986).

Due to the fact that weaver birds are colonial breeders, one tree can house approximately 100 nests located at various branch heights. Although weaver birds are a customary component of Hadza wet season diet, this phenomenon has not previously been reported. The hatchlings are exploited on a daily basis for only a short period of time, approximately five to eight weeks per year.

Figure 40: Young male forager with weaver birds strung on his bow

Both adults and children alike are able to collect several kilograms of weaver bird nestlings daily (Figure 40). A long stick is sharpened and then used to pull individual nests down from the branches. In addition to targeting nestlings, children in

this age group also target young birds that have recently left the nest. They prepare a stick (approximately 1 – 2 feet in length) with the sticky pulp of an inedible berry, called “rembo”. The “rembo” is then used like a paste and spread on the stick, which is placed in a small body of water, typically a watering hole. When the young weaver birds fly to the water to drink, several birds land on the stick, get stuck in the paste, and are then captured by the children waiting at the water’s edge. The birds are prepared on a small fire tended by the older girls in the foraging party and consumed by the entire group.

During the dry season, the bulk of energy is obtained from figs and baobab and supplemented with small mammals. As discussed above, figs and baobab are easy to collect; figs provide a substantial amount of energy. In addition, mice, the species of small mammal typically targeted by this age group, are abundant in camp and easy to shoot with small bows and arrows.

Foraging choices of adolescents in age group 4 (ages 14 - 17 years)

There are no significant seasonal differences in the amount of kilocalories collected among adolescents in age group 4 (14 – 17 years), however the type of food

targeted changes with seasonal availability. Baobab is collected all year, however during the wet season adolescents are obtaining the most kilocalories from the collection of birds, tubers, and honey. During the dry season this shifts to baobab, drupes, figs, and legumes; these are foods only collected by foragers in this age category. Legumes and drupes both require boiling before consumption, a task typically executed by adolescents who are more experienced fire preparation than their younger counterparts. Drupes and baobab provide approximately the same amount of energy per 100g fresh weight (Table 5). Legumes are relatively low in energy value, however they contain almost 25% protein (see chapter 3).

Sex differences in foraging

Sex has an effect on the type and amount of food brought back to camp. During the wet season male foragers bring back significantly more kilocalories than female foragers, which may be associated with the abundance of weaver birds that are collected during the wet season. Young male foragers focus the bulk of their wet season collection on these easy to obtain snack-sized packages of protein and supplement with honey and baobab. Female foragers, although they also target weaver

birds, tend to focus their wet season collection on tubers, berries, and birds. During the dry season, female foragers bring back more kilocalories than their male counterparts. Female foragers focus their efforts on figs and baobab, whereas male foragers focus their effort on hunting small mammals and collecting baobab.

If the year round profile (across seasons) is considered, female children tend to focus their collection on figs, baobab, tubers, and berries. Male children also collect baobab to a lesser extent, yet tend to primarily target birds, small mammals, and honey. These results are strikingly similar to sex differences in collection among Hadza adults (Crittenden et al. 2003; Marlowe 2007).

When analyzing the year round pattern, both seasons combined, there are no sex differences in the overall amount of food brought back to camp, however female children tend to bring more food back to camp when foraging in a group. Both female and male children travel approximately the same distance when out foraging. One male forager, aged 14 years (Table 6, forager 13), was an extraordinary hunter and honey collector and represents the only outlier. He traveled the farthest distance from camp and spent the longest time out of camp on foraging excursions; his longest outing was approximately seven kilometers round trip and over five hours in length.

Male children also consume significantly more than female children while out of camp on a foraging trip. One child, aged 10 years (Table 6, forager 8), consumed upwards of 3,000 kcal of honey in one three hour focal follow. He borrowed his father's axe and left camp in search of a hive. He brought no honey back to camp to share and consumed the entirety of his yield while standing in the tree at the hive. Sex differences in consumption may be associated with sex differences in foraging strategies.

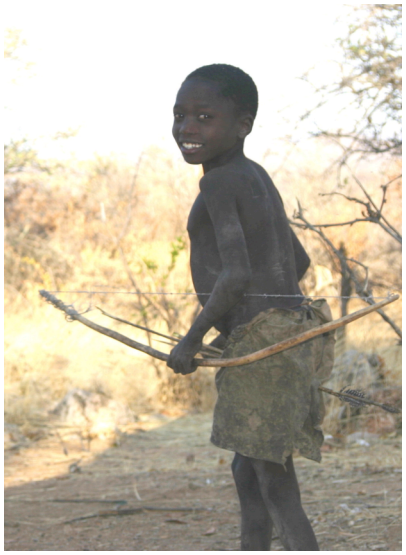

Figure 41: Young hunter with his bow

Armed with a bow and arrows, and sometimes a small axe, male children leave camp targeting small game and honey. Honey collection and the hunting of small and medium sized game involve high energetic costs. Locating, climbing, and chopping into trees to access honey may require an increase in energy requirement that can be met with the energy provided by the simple sugars of liquid honey. Tracking animals may increase energy requirements; young Hadza hunters will snack on baobab pods and berries to curb their hunger while out during the day. Interestingly, the timing of solo foraging trips (Figure 41) by male children corresponds to the timing of when adolescent growth spurt begins. Based on consumption estimates and growth velocity curves of other foraging populations (Figures 42 and 43), young male Hadza foragers may be feeding the excess requirements of their own growth when eating large amounts of food outside of camp.

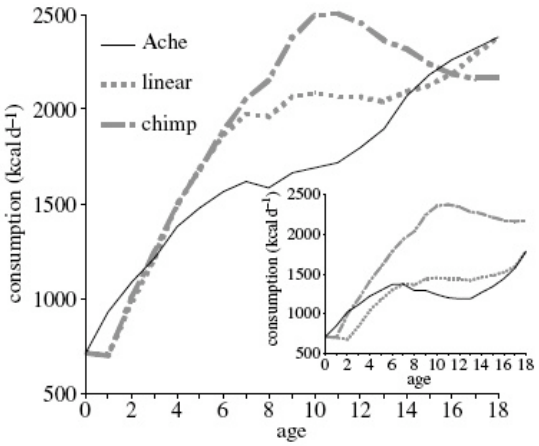

Figure 42: Consumption estimates by age for Ache and !Kung (inset) foragers undergoing observed, linear, and chimpanzee like growth. Averages for males and females combined. (From Gurven & Walker 2006)

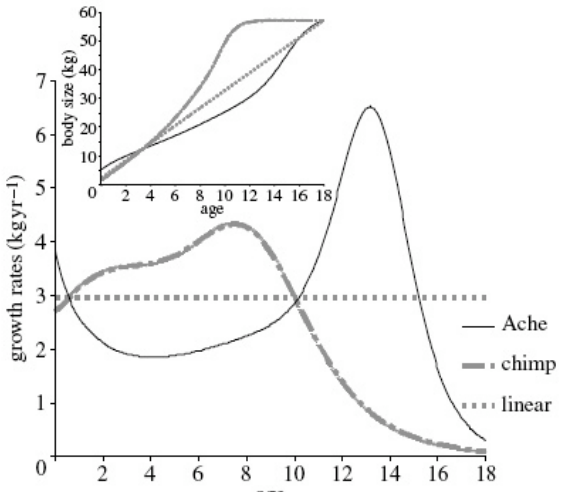

Figure 43: Growth velocity estimates based by age for Ache and !Kung (inset) male foragers undergoing observed, linear, and chimpanzee like growth. (From Gurven & Walker 2006)

Conclusions

The results presented here agree with previously published data on the foraging of Hadza children and adolescents, indicating that individuals above the age of five years are capable of collecting up to 50% of their daily energy requirement (Blurton Jones et al. 1989). The current study differs from previous findings, however, and focuses on foods collected without any adult supervision. This is the first study to characterize not only the types of foods targeted by young Hadza foragers but also quantify individual daily returns, measured in kilocalories per day. In addition, the analyses reported here are solely the collection of the individual forager and do not represent team rates combined with a mother's foraging yield (as reported in Hawkes et al. 1995).

Food returns are highly variable between foragers and in the daily return for an individual forager. An individual's daily return can greatly fluctuate depending on food type and individual motivation to leave camp to forage. Such wide variation in individual collection is consistent with published values on children's foraging on the Island of Mer (Bird & Bliege-Bird 2002; Bliege-Bird & Bird 2002), among the Martu of Australia (Bird & Bliege-Bird 2005), and the Mikea of Madagascar (Tucker &Young 2005).

When looking across the year (combining wet and dry season results), age does not affect the amount of food that a child is able to bring back on an individual foraging trip nor the total amount of food that a child can collect overall. Although individual foraging returns are highly variable, a child of five years can collect the same amount as a child of 16 years. These results are similar to those found among the children of Mer who exhibit no significant differences in mean foraging return rates across age categories above the age of five years (Bliege Bird and Bird 2002). Taken together, these data suggest that foraging skill does not necessarily increase with age, as predicted by Kaplan's model, and that differences in skill may have a stronger affect on foraging returns than age.

A handful of children appear to be more successful foragers than others. One twelve-year-old girl (Table 6 - forager 25) is an outlier in all of the analyses. On three foraging days her daily returns regularly exceeded 10,000 kilocalories, and even surpassed 11,000 kilocalories on a day of fig collection. Her younger sister, aged 6 (Table 6 - forager 19), also has uncharacteristically high returns and is capable of bringing back close to 7,000 kilocalories a day when collecting figs. They represent a unique case in which both parents are unable to routinely collect enough food to

provision every individual living in their home; their father has a severe debilitating injury from falling into a fire as a young child and their mother is developmentally delayed. The two sisters were not only able to provision themselves, but also shared their foraging yield with their younger brother, parents, and occasionally grandparents. Their younger brother, aged 3 (Table 6, forager 15) is the youngest child forager in the sample and the only individual representing age category 1 (1 - 4 years). The high yields of the children in this family may be linked to their individual ability and/or motivation to collect food. The wide variation in overall return that characterizes these data may be linked to the individual skill of the forager and the circumstances facing each child, rather than differences in yield based on age or sex.

The daily return averages for adolescents (Table 6) do not routinely meet daily energy requirements, however, data from focal follows suggests that young male foragers consume large amounts of food while out of camp. Female adolescents spend a large amount of time in camp caring for younger children (see chapter two) and also tend to be in charge of household chores, like water collection, during the day. Their investment may be in the form of household maintenance, rather than routine collection of large amounts of food. This follows the pattern among other foraging

groups suggesting that there is greater economic demand of the time of female adolescents when compared to their male counterparts (Ivey Henry et al. 2005). Future analysis of this data set will quantify the activity budgets of children and adolescents to determine the amount of time spent in various economic activities.

The results of this study suggest that Hadza children and adolescents are able to successfully provide a substantial portion of their own daily energetic requirements. Although they may not reach the age of positive net production until they are in their teenage years, any amount of food collection by young foragers assists in subsidizing their growth and development. Children's contributions may be one mechanism that allows mothers to maintain relatively short IBI, supporting the notion of humans as cooperative breeders.

Chapter 4, in part, is currently being prepared for submission for publication. The dissertation author was the primary investigator and author of this paper.

V. The Evolution of Cooperative Breeding in Humans

Mothers undertake this monumental task of raising multiple, highly dependent offspring with the assistance of allomothers who provide care and assistance, whether in the form of behavioral investment (i.e. babysitting) or provisioning (i.e. food back to camp). The assistance of allomaternal helpers has been linked to increased fertility of the recipient mother and greater survivorship and growth of her existing offspring (Bereczkei & Dunbar 1997, 2002; Crognier et al. 2001, 2002; Flinn 1989; Ivey 2000; Sear et al. 2000, 2002; Turke 1988). The current study analyzes allomaternal investment among the Hadza foragers of Tanzania to determine the extent to which individuals invest in the children of others. Investment by a wide range of helpers sets the stage for classifying humans as cooperative breeders.

Conclusions – Allomaternal Holding

Among the Hadza mothers hold their infants the most, however a wide range of individuals provide care. Analysis of relatedness supports Hamilton's Rule, which proposes nepotism as the primary motivation to provide care. Fathers and maternal grandmothers are the primary caregivers among the constellation of potential

allomaternal helpers, however when controlling for residency (i.e. only analyzing cases where paternal grandmother is living in camp) paternal grandmothers also tend to hold their grandchildren frequently.

Using detailed information on residency and kinship patterns the kin selection hypothesis is supported. The degree of biological relatedness is positively correlated with a high degree of allomaternal holding. Children are held by related allomothers (all kin members including those individuals who are distantly related), more frequently than unrelated allomothers. In addition, a higher degree of relatedness between the holder and the child associates with a higher percent of time spent holding. These results indicate that nepotistic investment appears to be the primary motive for allomothering among the Hadza.

Further, data on very young allomothers holding other children suggests that the costs of holding a one year old child might be quite high for a four year old allomother. The limitations of applying the kin selection hypothesis notwithstanding, the evidence provided in the current study suggests that nepotism is a factor influencing the amount of care provided.

Kin selection alone, however, does not explain all of the investment because unrelated individuals also provide a substantial amount of care, at times spending over 12% of their time in camp holding children (Table 2). The motivation for providing care to genetically related individuals is straightforward, however the motives for providing substantial care to unrelated children remains less clear.

Motivations may include friendship and strengthening social bonds, learning to mother, reciprocity, and coercion (Hrdy 2005a). The present study shows that juvenile helpers ranging in ages from 1.5 – 17.9 years old provide a substantial amount of care and may spend up to 20% of their time in camp holding both related and unrelated children. The very young allomothers (1.5 years) are being supervised and minded by older allomothers. The findings do not reject the hypothesis that unrelated juveniles are providing care to gain practice in child rearing, but they may simply be exploited for their labor (coercion). For instance, one Hadza mother tied infant in a sling to a protesting unrelated young girl. Although the unrelated helper was objecting, the mother reprimanded the girl and walked away, leaving the child with no other choice but to provide care to the infant or face the consequences.

The data in this study show clearly that a Hadza mother has a large pool of helpers to draw from; any of whom may release some of her time constraints by providing behavioral care for her children, thus supporting the Cooperative Breeding hypothesis

Conclusions– Juvenile Foraging

One additional class of helper available to Hadza mothers are juveniles who can contribute to their own care. Results presented here show that Hadza children and adolescents routinely collect a sizeable amount of a wide range of both plant and animal foods and are able to significantly contribute to the greater subsistence economy. The current study analyzed twenty-six samples of juvenile plant foods to determine the potential energy contribution of juvenile foods. Several of the fruit species, including baobab, figs, and berries, provide 100 – 200 kcal/100g fresh weight. In addition, the small mammals, birds, and legumes targeted by juveniles are high in protein.

There are significant age and sex differences in the type of foods targeted. During the wet season, young children tend to focus on foods that are easier to collect

and process, such as baobab and figs, which allows them to collect significantly more kilocalories when compared to the dry season. During the dry season they focus on berries and tubers, which are more difficult to find, collect, and process. Older children collect baobab throughout the year, but also incorporate figs, birds, honey, tubers, and berries. In addition, legumes and drupes are collected in small amounts; these foods are only collected by older adolescent children because they are difficult to obtain and require more processing.

Age and sex do not appear to affect overall food collection yields; a young forager of six years is able to bring back the same amount of food as a forager of sixteen years. Older children and adolescents require more food than their younger counterparts, however their average daily yields are not dissimilar. This may be due to the fact that an adolescent's time (especially that of a young female forager) is in great demand. Female adolescents are in charge of maintaining peace among the younger children during the day, collecting and distributing water, creating and tending to cooking fires, and taking responsibility of any other household chores. The high demands on their time might explain why the return rates for adolescents are not higher than those of children. It is not merely a matter of skill, but of time

management. Future analysis of this data set will explore the time budgets and energetic expenditures of young foragers.

The results presented here are the first to quantify overall daily production among juvenile foragers. In addition to weighing all of the food brought back, estimates on amounts of food consumed while out foraging were also recorded. Hadza children and adolescents are capable of successfully providing a substantial portion of their own daily intake, although only a handful of children appear to consistently collect large amounts of food.

There is a wide array of individual average daily returns, ranging from <50 - >2500 kilocalories. Some children appear to be more motivated to collect larger amounts of food. Two girls in the sample routinely collect food that provides between 7,000 and 10,000 kilocalories per day and are able to provision themselves, their younger siblings, and occasionally their parents and grandparents. The implications of such a wide range of daily production values indicate that food returns are more greatly influenced by individual circumstance than age or sex specific skill levels.

The flexible nature of human foraging strategies has created an opportunity for juvenile food collection and self-provisioning that lessens constraints on maternal

investment. Food contributions by children and adolescents underwrite the cost of their own care, thereby decreasing some of the energetic burden faced by mothers with multiple dependent offspring.

The Evolution of Cooperative Breeding in Humans

Allomaternal support may take various forms. The data presented in this analysis highlight two pathways of contributed care that lend support to the notion of humans as cooperative breeders: direct behavioral investment (i.e. holding) and self-provisioning of juvenile foragers.

In our evolutionary history, the wide range of individuals identified here who clearly offer support in the form of caretaking and provisioning could have allowed the population of early hominids to expand. A shift in subsistence behavior that included contributions of group members other than the mother would have been necessary. Using fossil evidence of tooth formation and eruption and endocranial volume, it has been suggested that a pattern of life history similar to modern humans may have been present in early species of *Homo* (Robson & Wood 2008).

Early weaning and late age at maturity may have allowed Pleistocene mothers to increase the number of offspring that they produced over a lifetime. Help from family and friends may have allowed for a capacity for population growth that was not necessarily a rapid increase in numbers, but merely allowed groups to recover from population bottlenecks (Washburn 1981; Zeller 1987). This flexibility in subsistence behavior and childcare patterns would permit a hominid mother to thrive in any ecological setting, a characteristic highlighting human behavioral diversity.

Appendix 1 – Non-parametric Statistical Analyses for Chapter 2

In addition to analyzing proportions (percent of scans in which people were holding), we also analyzed counts of holding using non-parametric tests in which instances of holding were weighted by number of observations, giving greater weight to those individuals who appeared in more scans. Due to the fact that we used counts of observations and included every instance of holding, our sample sizes were larger than the sample sizes used in the proportional data analysis. Nearly all of the results were replicated using the non-parametric analyses. The only result that differed was the amount of time female and male allomothers spent holding children. Using counts of holding, female allomothers spent significantly more time holding children than male allomothers (Wilcoxon rank sum $W = 1952$, $p = .02$). The difference in results may be explained by the difference in sample sizes.

All of the following tests yielded the same results as when using proportional data. The sex of a child was not associated with the amount of time a child was held (Wilcoxon rank sum $W = 808$, $p = 0.90$) and younger children were held significantly more often than older children ($R^2 = .55$, $p < .0005$, the dependent variable is the log frequency of being held). Children were held by related allomothers significantly more often than unrelated allomothers (Wilcoxon sign rank $V = 1089$, $p = .02$, $n_1 = 42$

related, $n_2 = 39$ unrelated; from the point of view of the child) and more frequently by maternal relatives than paternal relatives (Wilcoxon sign rank V = 386, $p < 0.05$, n= 75 children < 4 years). When controlling for residency in camp, maternal grandmothers did not hold significantly more than paternal grandmothers (Wilcoxon rank sum W = 165, p = .64). For the child, the presence of maternal grandmothers and fathers in camp were not independent (Pearson's Chi Square x^2 (1, n = 75) = 13.07, p < .05).

Two separate analyses were performed in order to determine whether holding was a product of kin selection. First, pooled proportions (all counts of allomaternal holding – mother excluded) were used to perform a logistic fit over the three levels of relatedness (.5, .25, and .125 as predictors). Under the assumption of logistic relationship, degree of relatedness is a significant predictor ($p < .0005$) of holding. The second analysis is a difference-of-proportions test involving two separate comparisons across the three levels of degree of relatedness. Individuals who are .5 degree of relatedness are holding significantly more than individuals who are .25 degree of relatedness ($X^2 = 6.65$, $p < 0.0005$). Individuals who are .25 degree of relatedness are holding more than individuals who are .125 degree of relatedness ($X^2 = 94.21$, p <

.0005). In order to control for age of the child, regression was used to determine if the inclusion of age was lessening the effect that the degree of relatedness had on the frequency of being held. In both cases it did not.

References

Addy, E.O. and E. Eteshola (1984) Nutritive value of a mixture of tigernut tubers (*Cyperus esculentus* L.) and baobab seeds (*Adansonia digitata* L.). *Journal of the Science of Food and Agriculture* 35: 437-440.

Asa, C.S. (1997) Hormonal and experiential factors in the expression of social and parental behavior in canids. In *Cooperative Breeding in Mammals*, N.G. Solomon and J.A. French, eds. Pp. 129-149. Cambridge: Cambridge University Press.

Alvarez , H.P. (2000) Grandmother hypothesis and primate life histories. *AmericanJournal of Physical Anthropology* 113(3): 435-450.

Association of Official Analytical Chemists (AOAC) (1984) Fat (crude) or ether extract in animal feeds: direct method. In Official methods of analysis of the Association of Official Analytical Chemists, S. Williams, ed. Pp. 159-160. Arlington, Virginia: Association of Official Analytical Chemists.

Barry, H.A. and L.N. Paxson (1971) Infancy and early childhood: Cross-cultural codes. *Ethnology* 10: 466-500.

Bereczkei, T. (1998) Kinship network, direct childcare, and fertility among Hungarians and Gypsies. Evolution and Human Behavior 19(5): 283-298.

Bendor, J. and P. Swistak (1997) The evolutionary stability of cooperation. *American Political Science Review* 91 pp. 290–307.

Bereczkei, T. and R.I.M. Dunbar (1997) Female-biased reproductive strategies in a Hungarian Gypsy population. *Proceedings of the Royal Society of London Series B* 264: 17-22.2002Helping-at-the-Nest and Sex-Biased Parental Investment in a Hungarian Gypsy Population. *Current Anthropology* 43: 804-810.

Bergman, E.N. (1990) Energy contributions of volatile fatty acids from the gastrointestinal tract in various species. *Physiological Reviews* 70: 567-590.

Bird, D. and R. Bliege-Bird (2005) Martu Children's Hunting Strategies in the Western Desert, Australia. In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp. 129-146. Piscataway: Aldine Transaction

Bliege-Bird, R. and D. Bird (2002) Constraints of knowing or constraints of growing? Fishing and collecting by the children of Mer. *Human Nature* 13: 239-267.

Blurton Jones, N.G. (1993) The lives of hunter-gatherer children: effects of parental behavior and parental reproductive strategy. In *Juvenile Primates – Life History, Development, and Behavior*, M.E. Pereira, L.A. Fairbanks, eds. Pp. 309-326. New York/Oxford: Oxford University Press.

Blurton Jones, N.G., F.W. Marlowe, K. Hawkes, and J. O'Connell (2000) Paternal investment and hunter-gatherer divorce rates, In *Adaptation and Human Behavior: An Anthropological Perspective*, L. Cronk, N. Chagnon, and W. Irons, eds. Pp. 69-90. New York: Elsevier.

Blurton Jones, N.G., K. Hawkes, and P. Draper (1994) Differences between Hadza and !Kung children's work: Affluence and Practical Reason? In *Key Issues in Hunter-Gatherer Research*, E.S. Burch Jr. and L.J. Ellanna, eds. Pp 189-215. Oxford: Berg.

Blurton Jones, N.G., K. Hawkes, and J.F. O'Connell (1989) Modeling and measuring costs of children in two foraging societies. In *Comparative Socioecology*, V. Standen and R.A. Foley, eds. Pp. 367-390. Oxford: Blackwell Scientific.

Blurton Jones, N.G., K. Hawkes, and J.F. O'Connell (1997) Why do Hadza children forage? In *Uniting Psychology and Biology: Integrative Perspectives on Human Development*, N. Segal, G.E. Weisfeld, and C.C. Weisfeld, eds. Pp 279-313. Washington, D.C.: American Psychological Association.

Blurton Jones, N.G., K. Hawkes, and J.F. O'Connell (2005) Older Hadza Men and Women as Helpers: Residence Data. In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp. 214-236. Piscataway: Aldine Transaction.

Blurton Jones, N. B. and F.W. Marlowe (2002) Selection for delayed maturity: Does it take 20 years to learn to hunt and gather? *Human Nature* 13(2): 199-238.

Blurton Jones, N., L.C. Smith, J.F. O'Connell, K. Hawkes, and C.L. Kamuzora (1991) Demography of the Hadza, an increasing and high density population of savanna foragers. *American Journal of Physical Anthropology* 89 (2): 159-181.

Bock, J. (2002) Learning, Life History, and Productivity: Children's lives in the Okavango Delta of Botswana. *Human Nature* 13(2): 161-198.

Bock, J. and S.E. Johnson (2004) Subsistence ecology and play among the Okavango Delta people of Botswana. *Human Nature* 15: 63-81.

Boesch, C. and Boesch-Achermann, H. (2000) *The Chimpanzees of the Tai Forest: Behavioral Ecology and Evolution*. Oxford: Oxford University Press.

Bogin, B. (1997) Evolutionary hypotheses for human childhoods. *Yearbook of Physical Anthropology* 40: 63-89.

Bogin, B. (2008) *Patterns of Human Growth*. Second Edition. London: Cambridge University Press.

Bogin, B. and B.H. Smith (1995) Evolution of the Human Life Cycle. *American Journal of Human Biology* 8(6): 703-716.

Borgerhoff-Mulder, M. and M. Milton (1985) Factors affecting infant care in Kipsigis. *Journal of Anthropological Research* 41: 231-262.

Bove, R.B., C.R. Valeggia, and P.T. Ellison (2002) Girl Helpers and Time Allocation of Nursing Women among the Toba of Argentina. *Human Nature* 13(4): 457-472.

Brewer-Marsden, S., D. Marsden, and M. Emery Thompson (2006) Demographic and female life history parameters of free-ranging chimpanzees at the Chimpanzee Rehabilitation Project, River Gambia National Park. *International Journal of Primatology* 27: 391-410.

Britton, P.L. (1980) *Birds of East Africa: Their habitat, status, and distribution*. Nairobi: East African Natural History Society.

Bugaut, M. (1987) Occurrence, absorption, and metabolism of short chain fatty acids in the digestive tract of mammals. Comparative Biochemistry and Physiology Part B - Biochemistry and Molecular Biology 86 (3): 349-472.

Bunn, H., L.E. Bartram, and E.M. Kroll (1988) Variability and bone assemblage formation from Hadza hunting, scavenging, and carcass processing. Journal of Anthropological Archaeology 7: 412:457.

Busson, F. (1965) *Plantes alimentaires de l'ouest africain*. L'Imprimerie. Marseille: Leconte.

Charnov, E.L. and D. Berrigan (1993) Why do female primates have such long life spans and so few babies? Or life in the slow lane. Evolutionary Anthropology 1: 191-194.

Chowning, A. (1972) Child rearing and socialization. In *Encyclopedia of Papua New Guinea*, P. Ryan, Ed. Melbourne: University Press.

Clum, N.J., M.P. Fitzpatrick, and E.S. Dierenfeld (1996) Effects of diet on nutritional content of whole vertebrate prey. Zoo Biology 15(5): 525-537.

Clutton-Brock, T. H. (1991) *The Evolution of Parental Care*. Princeton, NJ: Princeton University Press.

Clutton-Brock, T. H. (2002) Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates. *Science* 296: 69-72.

Clutton-Brock, T.H., P.N.M. Brotherton, M.J. O'Riain, A.S. Griffin, D. Gaynor, L.L. Sharpe, R. Kansky, M. Manser and G.M. McIlrath (2000) Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society of London Series B* 267: 301-305.

Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* 29: 141-177.

Conklin, N.L. and R.W. Wrangham (1994) The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. *Biochemical Systematics and Ecology* 22(2): 137-151.

Conklin-Brittain, N.L., R.W. Wrangham, and K.D. Hunt (1998) Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. II. Macronutrients. *International Journal of Primatology* 19(6): 949-970.

Conklin-Brittain, N.L., C.D. Knott, and R.W. Wrangham (2006) Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In *Feeding Ecology in Apes and Other Primates: Ecological, Physical, and Behavioral Aspects*. G. Hohmann, M.M. Robbins, and C. Boesch, eds. Pp 445-471. Cambridge: Cambridge University Press.

Crittenden, A.N. and F.W. Marlowe (2008) Allomaternal care among the Hadza of Tanzania. *Human Nature* 19: 249-262.

Crittenden, A.N., Richardson, M.R., Schoeninger, M.J., Bunn, H.T., and Pickering, T.R. (2003) Differential Foraging Strategies of Hadza Men and Women. American Journal of Physical Anthropology 120(S36), poster to be presented at the Seventy-Second Annual Meeting of the American Association of Physical Anthropologists.

Crognier, E., A. Baali, and M.K. Hilali (2001) Do "helpers at the nest" increase their parents' reproductive success? *American Journal of Human Biology* 13(3): 365-373.

Crognier, E., M. Villena, and E. Vargas (2002) Helping patterns and reproductive success in Aymara communities. *American Journal of Human Biology* 14(3): 372-379.

Davies, N. (1992) *Dunnock Behaviour and Social Evolution*. Oxford: Oxford University Press.

Denham, W. (1974) Infant transport among the Alyawara tribe, Central Australia. *Oceania* 64 (4): 253-277.

Dittami, J.P. (1986) Seasonal reproduction, moult, and their endocrine correlates in two tropical *Ploceidae* species. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* 165(5): 641-647.

Draper, P. and E. Cashdan (1988) Technological change and child behavior among the !Kung. *Ethnology* 27(4): 339-365.

Draper, P. and H. Harpending (1987) Parent investment and the child's environment. In *Parenting Across the Lifespan: Biosocial Dimensions*, J. B. Lancaster, A. Rossi, J. Altmann, and L. Sherrod, Eds. Pp. 187-205. New York: Aldine.

Dubois, M., K.A. Giles, J.K. Hamilton, P.A. Rebers, and F. Smith (1956) Colorimetric methods for determination of sugars and related substances. *Analytical Chemistry* 28: 350-356.

Dugatkin, L.A. (1997) *Cooperating among Animals*. New York: Oxford University Press.

Dwyer, P.D. (1974) The price of protein: five hundred hours of hunting in the New Guinea highlands. *Oceania* 55: 278-293.

Emlen, S.T. (1994) Benefits, Constraints, and the Evolution of the Family. *Trends in Ecology and Evolution* 9: 282-285.

Emlen, S.T. and P.H. Wrege (1989) A test of alternate hypotheses for helping behavior in white-fronted bee-eaters of Kenya. *Behavioral Ecology and Sociobiology* 25(5): 303-319.

Euler, H.A. and B. Weitzel (1996) Discriminative grandparental solicitude as reproductive strategy. *Human Nature* 7: 39-60.

Fletcher, A.W. (2001) Development of infant independence from the mother in wild mountain gorillas. In *Mountain Gorillas: Three Decades of Research in Karisoke*, M.M. Robbins, P. Sicotte, and K. Stewart, eds. Pp. 158-182. Cambridge: Cambridge University Press.

Flinn, M.V. (1989) Household composition and female reproductive strategies in a Trinidadian village. In *The Sociobiology of Sexual and Reproductive Strategies*, A.E. Rasa, C. Vogel, and E. Voland, eds. Pp. 206-233. London: Chapman and Hall.

Fosbrooke, H.A. (1956) A stone age tribe in Tanganyika. The South African Archaeological Bulletin 11 (41): 3 – 8.

Foster, K.R., T. Wenseleers, and F.L.W. Ratnieks (2006) Kin selection is the key to altruism. *Trends in Ecology and Evolution* 21 (2): 57-60.

Fouts, H. and M.E. Lamb (2005) Weanling Emotional Patterns among the Bofi Foragers of Central Africa: The Role of Maternal Availability and Sensitivity. In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp. 309-321. Piscataway: Aldine Transaction.

French, J.A. (1997) Proximate regulation of singular bleeding in callitrichid primates. In *Cooperative Breeding in Mammals*, N.G. Solomon and J.A. French, eds. Pp. 34-75. Cambridge: Cambridge University Press.

Garber, P.A. and S.R. Leigh (1997) Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatologica* 68 (1): 1-22.

Garrow, J.S. (1978) *Energy Balance and Obesity in Man*, 2nd Edition. Amsterdam: Elsevier/North Holland.

Gotts, N.M., J.G. Polhill and A.N.R. Law (2003) Agent-based simulation in the study of social dilemmas. *Artificial Intelligence Review* 19 pp. 3–92.

Grafen, A. (1984) Natural selection, kin selection, and group selection. In *Behavioural Ecology: An Evolutionary Approach*, J. Krebs and N. Davies, eds. Pp. 62-84. Oxford: Blackwell Scientific Publications.

Griffin, A.S. and S.A. West (2002) Kin Selection: fact and fiction. *Trends in Ecology and Evolution* (17) 1: 15-21.

Gurven, M. and R. Walker (2006) Energetic demand of multiple dependents and the evolution of slow human growth. *Proceedings of the Royal Society B* 273: 835-841.

Gusinde, M. (1931) *Die Feuerland-Indianer, Band I. Die Selk'nam*. Modling bei Wien: Anthropos.

Hames, R. (1988) The allocation of parental care among the Ye'kawana. In *Human Reproductive Behavior*, ed. By Laura Betzig, Monique Borgerhoff Mulder, and Paul Turke, pp. 237-251. Cambridge: Cambridge University Press.

Hamilton, W.D. (1964) The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7: 1-18.

Harrison, G.A., J.M. Tanner, D.R. Pilbeam, and P.T. Baker (1993) *Human biology: An introduction to human evolution, variation, and growth and adaptability.* Oxford: Oxford Science Publications.

Hawkes, K. (1991) Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology* 12:29-54.

Hawkes, K (1997) Hadza women's time allocation, offspring production, and the evolution of long postmenopausal life spans. *Current Anthropology* 38: 551-577.

Hawkes, K. (2006) Slow life histories and human evolution. In *The Evolution of Human Life History*, K. Hawkes and R.R. Paine, eds. Pp. 95-126. Santa Fe: School of American Research Press.

Hawkes, K., J.F. O'Connell, and N. Blurton Jones (1989) Hardworking Hadza Grandmothers. In *Comparative Socioecology of humans and other mammals*, V. Standen and R.A. Foley eds. Pp 341-366. London: Basil Blackwell.

Hawkes, K., J.F. O'Connell, and N. Blurton Jones (1995) Hadza children's foraging: Juvenile dependency, social arrangements and mobility among hunter-gatherers. Current Anthropology 36(4): 688-700.

Hawkes, K., J.F. O'Connell, N.G. Blurton-Jones, E.L. Charnov, and H. Alvarez (1998) Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences* 9: 1336-1339.

Healey, C. (1990) *Maring hunters and traders: Production and exchange in the Papua New Guinea Highlands*. Berkeley: University of California Press.

Heinsohn, R. and M.C. Double (2004) Cooperate or speciate: new theory for the distribution of passerine birds. *Trends in Ecology & Evolution* 19(2): 55-57.

Hewlett, B.S. (1991) Demography and Childcare in Preindustrial Societies. *Journal of Anthropological Research* 47: 1– 37.

Hewlett, B.S. and M.E. Lamb (2005) *Hunter-Gatherer Childhoods.* Piscataway: Aldine Transaction.

Hill, K. and Hurtado, M. (1996) *Ache Life History: The Ecology and Demography of a Foraging People*. Hawthorne, NY: Aldine de Gruyter.

Holden, J.M., Pehrsson, P.R., Perry, C., Patterson, K.K., Haytowitz, D.B (2006) Understanding nutrient variability: impact on public health. National Nutrient Databank Conference, September 18-20, 2006, Hawaii.

Holden, J.M., Pehrsson, P.R. (2008) Development of sampling strategies for foods in Latin America. FAO Food Sampling Workshop, February 23-March 1, 2008, Tucuman, Argentina.

Howell, N. (1979) *Demography of the Dobe !Kung*. New York: Academic Press.

Hrdy, S.B. (1999) *Mother Nature: A History of Mothers, Infants, and Natural Selection*. New York: Pantheon Books.

Hrdy, S.B. (2005a) Comes the Child Before Man: How Cooperative Breeding and Prolonged Post-Weaning Dependence Shaped Human Potentials. In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp. 65-91. Piscataway: Aldine Transaction.

Hrdy, S.B. (2005b) Evolutionary Context of Human Development: The Cooperative Breeding Model. In *Attachment and Bonding: A New Synthesis*, C.S. Carter, L. Ahnert, eds. Pp. 9-32. Cambridge: MIT Press.

Hrdy, S.B. (2009) *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Cambridge, MA. Harvard University Press.

Hruschka, D.J. and J. Henrich (2006) Friendship, cliquishness, and the emergence of cooperation. *Journal of Theoretical Biology* 239 (1): 1-15.

Institute of Medicine of the National Academies (2002) Dietary Reference Intakes for Energy, Carbohydrate, Fiber, Fat, Fatty Acids, Cholesterol, Protein, and Amino Acids. Washington, DC: National Academies Press.

Ivey, P.K. (2000) Cooperative Reproduction in the Ituri Forest Hunter-Gatherers: Who cares for Efe Infants? *Current Anthropology* 41: 856-866.

Ivey, P.K., G.A. Morelli, and E.Z. Tronick (2005) Child Caretakers Among Efe Foragers of the Ituri Forest. In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp. 191-213. Piscataway: Aldine Transaction.

Jarvis, J.U.M., J. O'Riain, N.C. Bennet, and P.W. Sherman (1994) Mammalian eusociality: a family affair. *Trends in Ecology and Evolution* 9:47-51.

Kaare, B. (1994) The impact of modernization policies on the hunter-gatherer Hadzabe: The case of education and language policies of postindependence Tanzania. In Key Issues in Hunter-Gatherer Research, E. Burch and L. Ellan, eds. Pp. 315-331. Oxford: Berg Publishers.

Kaplan, H., K. Hill, and A. Hurtado (1984) Food sharing among the Ache hunter-gatherers of eastern Paraguay. *Current Anthropology* 25: 113-115.

Kaplan, H. (1994) Evolutionary and wealth flows theories of fertility: Empirical tests and new models. Population and Development Review 20: 753-791.

Kaplan, H. (1997) The Evolution of the Human Life Course. In *Between Zeus and Salmon: The Biodemography of Longevity*, KI. Wachter and C. Finch, eds. Pp 175-211. Washington, D.C.: National Academy of Sciences.

Kaplan, H.S., K.R. Hill, J.B. Lancaster, A.M. Hurtado (2000) A Theory of Human Life History, Evolution: Diet, Intelligence, and Longevity. *Evolutionary Anthropology* 9: 156-185.

Kaplan, H.S., K.R. Hill, J.B. Lancaster, A.M. Hurtado (2001) The embodied capital theory of human evolution. In *Reproductive Ecology and Human Evolution*, P.T. Ellison, ed. Hawthorne, NY: Aldine de Gruyter.

Kennedy, G.E. (2005) From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. Journal of Human Evolution 48: 123-145.

Knott, C. (2001) Female reproductive ecology of the apes: Implications for human evolution. In *Reproductive Ecology and Human Evolution*, P. Ellison Ed. Pp. 429-463. New York: Aldine de Gruyter.

Kokko, H., R.A. Johnstone, and J. Wright (2001) The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behavioral Ecology* 13 (3): 291-300.

Konig, B. (2006) Non-offspring nursing in mammals: general implications from a case study on house mice. In *Cooperation in Primates and Humans*, P. M. Kappeler, and C. P. van Schaik, eds. Pp. 191-208. Berlin: Springer.

Konner, M.J. (1976) Maternal care, infant behavior and development among the !Kung. In *Kalahari Hunter-Gatherers: Studies of the !Kung San and their Neighbors*, R.B. Lee and I. DeVore, eds. Pp. 218-245. Cambridge: Cambridge University Press.

Konner, M.J. (1977) Infancy among the Kalahari Desert San. *In Culture and Infancy: Variations in the Human Experience*, P.H. Leiderman, S.R. Tulkin, and A. Rosenfeld, eds. Pp. 287-328. New York: Academic Press.

Konner, M.J. (2005) Hunter-Gatherer Infancy and Childhood: The !Kung and Others. In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp.19-64. Piscataway: Aldine Transaction.

Kramer, K.L. (2002) Variation in juvenile dependence: Helping behavior among Maya children. Human Nature 13(2): 299-325.

Kramer, K.L. (2004) Reconsidering the cost of childbearing: The timing of children's helping behavior across the life cycle of Maya families. In *SocioEconomic Aspects of Human Behavioral Ecology, Research in Economic Anthropology (Volume 23)*, M. Alvard, ed. Pp. 335-353. Amsterdam: Elsevier.

Kramer, K.L. (2005a) *Maya Children: Helpers at the Farm*. Cambridge, MA: Harvard University Press.

Kramer, K.L. (2005b) Children's Help and the Pace of Reproduction: Cooperative Breeding in Humans. *Evolutionary Anthropology* 14: 224-237.

Kramer, P.A. (1998) The costs of human locomotion: maternal investment in child transport. *American Journal of Physical Anthropology* 107:71-85.

Kurland, J. and J. Sparks (2003) Is there a Paleolithic demography? Implications for evolutionary psychology and sociobiology. Paper presented at the 15th Annual

Meeting of the Human Behavioral and Evolution Society Meetings, Lincoln, Nebraska: Jan. 4 – 8, 2003.

Kuroda, S. (1989) Developmental retardation and behavioral characteristics in the pygmy chimpanzee. In *Understanding Chimpanzees*, P.G. Heltne and L. Marquardt, eds. Pp. 184-193. Cambridge, MA: Harvard University Press.

Lancaster, J.B. (1971) Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica* 15 (3): 163-182.

Lancy, D.F. (1996) *Playing on the mother ground: Cultural routines for children's development*. New York: Guilford Press.

Lee, R.B. (1979) *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge: Cambridge University Press.

Lee, P.C., P. Majluf, and I.J. Gordon (1991) Growth, weaning, and maternal investment from a comparative perspective. *Journal of Zoology* 225: 99-114.

Leonetti, D., D. C. Nath, N.S. Hemam, and D. B. Neill (2002) Cooperative breeding effects of among the matrilineal Khasi of N.E. India. Paper presented at Human Behavior and Evolution Society Meetings, Rutgers University, Newark, New Jersey.

Leonetti, D., D. C. Nath, N.S. Hemam, and D. B. Neill (2005) Kinship organization and grandmother's impact on reproductive success among the matrilineal Khasi and patrilineal Bengali of N.E. India. In *Grandmotherhood: The Evolutionary Significance of the Second Half of Female Life*, E. Voland, A. Chasiotis, and W. Schiefenhoevel, eds. Pp. 194-214. Piscataway: Rutgers University Press.

LeVine, R., S. Dixon, S. LeVine, A. Richman, P.H. Leiderman, C. Kefer, and T.B. Brazelton (1996) *Child Care and Culture: Lessons from Africa*. New York: Cambridge University Press.

Ligon, J.D. and S.H. Ligon (1978) Communal breeding in green woodhoopoes as a case for reciprocity. *Nature* 276: 496-498.

MacDonald, K. (2007) Cross-cultural Comparison of Learning in Human Hunting: Implications for Life History Evolution. *Human Nature* 18: 386-402.

Mace, R. and R. Sear (2005) Are Humans Cooperative Breeders? In *Grandmotherhood: The Evolutionary Significance of the Second Half of Female Life,* E. Voland, A. Chasiotis, and W. Schiefenhoevel, eds. Pp. 194-214. Piscataway: Rutgers University Press. Markovits, H., J.F. Benenson and D.L. Kramer

Mace, R. and R. Sear (2003) Children and adolescents' internal models of food-sharing behavior include complex evaluations of contextual factors. Child Development 74, pp. 1697–1708.

Marlett, J. (1992) Content and composition of dietary fiber in 117 frequently consumed foods. Journal of the American Dietary Association 92: 175-186.

Marlowe, F.W. (1999) Male care and mating effort among Hadza foragers. *Behavioral Ecology and Socioecology* 46 (1): 57-64.

Marlowe, F.W. (2001) Male contribution to diet and female reproductive success among foragers. *Current Anthropology* 42 (5): 755-760.

Marlowe, F.W. (2002) Why the Hadza are still hunter-gatherers. In Ethnicity, Hunter-gatherers, and the "Other": Association or Assimilation in Africa, S. Kent, ed. Pp. 247-275. Washington, DC: Smithsonian Institution Press.

Marlowe, F.W. (2003) A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior* 24 (3): 217-229.

Marlowe, F.W. (2004) Marital residence among foragers. *Current Anthropology* 45: 277-284.

Marlowe, F.W. (2005) Who Tends Hadza Children? In *Hunter-Gatherer Childhoods*, B.S. Hewlett and M.E. Lamb, eds. Pp. 177-190. Piscataway: Aldine Transaction.

Marlowe, F.W. (2007) Hunting and gathering: The human sexual division of foraging labor. *Cross Cultural Research* 41: 170-195.

Marshall, L. (1976) *The !Kung of Nyae Nyae*. Cambridge, MA: Harvard University Press.

Martin, J.A., B.E. Hamilton, P.D. Sutton, S.J. Ventura, F. Menacker, and M.L. Munson (2003) Births: Final data for 2002. National Vital Statistics Reports volume 52, number 10. Hyattsville, MD: National Center for Health Statistics.

Meehan, C.L. (2005) The Effects of Residential Locality on Parental and Alloparental Investment among the Aka Foragers of the Central African Republic. *Human Nature* 16 (1): 58-80.

McDowell, W. (1981) A brief history of Mangola Hadza. Mbulu District Development Directorate, Mbulu District, Arusha Region.

McKenna, J.J. (1987) Parental Supplements and Surrogates among Primates: Cross-Species and Cross-Cultural Comparisons. In *Parenting across the Life Span: Biosocial Dimensions*, J.B. Lancaster, J. Altmann, A. Rossi, and L. Sherrod, eds. Pp. 143-186. New York: Aldine de Gruyter.

Mitani, J. and D. Watts (1997) The evolution of non-maternal caretaking among anthropoid primates: Do helpers help? *Behavioral Ecology Sociobiology* 40: 213-220.

Munroe, R.H., R.L. Munroe, and H.S. Shimmin (1984) Children's work in our cultures: determinants and consequences. *American Anthropologist* 86: 369-379.

Murray, S., M.J. Schoeninger, H.T. Bunn, T.R. Pickering, and J.A. Marlett (2001) Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. *Journal of Food Composition and Analysis* 14: 3-13.

Nag, M.G., N.F. Whitehead, and R.C. Peet (1978) An anthropological approach to the study of the economic value of children in Java and Nepal. *Current Anthropology* 19: 293-306.

National Academy of Sciences (1980) *Recommended Dietary Allowances*, 9th Edition. Washington DC.

National Research Council (1989) Diet and Health: Implications for Reducing Chronic Disease Risk. Report of the Committee on Diet and Health, Food and Nutrition Board. Washington DC: National Academic Press.

Nishida, T, N. Corp, M. Hamai (2003) Demography, female life history, and reproductive profiles among chimpanzees of Mahale. *American Journal of Primatology* 59: 99-121.

Nour, A.A., B.I. Magboul, and N.H. Kheiri (1980) Chemical composition of baobab fruit (*Adansonia digitata*). *Tropical Science* 22: 383-388.

Nowell, A.A., and A.W. Fletcher (2007) Development of independence from the mother in *Gorilla gorilla gorilla*. *International Journal of Primatology* 28: 441-455.

O'Connell, J.F, K. Hawkes, K.D. Lupo, and N.G. Blurton Jones (2002) Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution* 43: 831-872.

Panter-Brick, C. (1989) Motherhood and subsistence work: The Tamang of rural Nepal. *Human Ecology* 17(2):205-228.

Parker, S.T. (1984) Playing for keeps: An evolutionary perspective on human games. In *Play in animals and humans*, P.K. Smith, ed. Pp. 271-294. Oxford: Blackwell.

Pennisi, E. (1999) Did Cooked Tubers Spur the Evolution of Big Brains? *Science* 283(5410): 2004-2005.

Pierce, W.C. and E.L. Haenisch (1947) *Quantitative Analysis*, 2nd Edition. London: John Wiley & Sons.

Prange, H.D., J.F. Anderson, and H. Rahn (1979) Scaling of skeletal mass to body mass in birds and mammals. *The American Naturalist* 113(1): 103-122.

Purvis, A. and P.H. Harvey (1995) Mammalian life history evolution: A comparative test of Charnov's model. *Journal of Zoology* 237: 259-283.

Ray, V.F. (1963) *Primitive pragmatists: The Modoc Indians of Northern California*. Seattle: University of Washington Press.

Redd, D.A. (1998) The Hadza and Kaguru of Tanzania: gender roles and privileges at two subsistence levels. Lambda Alpha Journal, Volume 28: 54-67.

Robson, S.L., C. van Schaik, and K. Hawkes (2006) The derived features of human life history. In *The Evolution of Human Life History*, R.L. Paine and K. Hawkes, eds. Pp. 17 – 44. Santa Fe: School of American Research Press.

Salami, L.I. and U.N. Okezie (1994) The nutritional composition and storage stability of millet (*Pennisetum americanum*) supplemented with varying levels of baobab (*Adansonia digitata*) flours. *Ecology of Food and Nutrition* 31: 211-218.

Schoeninger, M.J. (2001) Hungry Hadza Grandmothers. *Journal of Human Evolution* 40: 19-20.

Schoeninger, M.J., H.T. Bunn, S.S. Murray, and J.A. Marlett (2001) Composition of Tubers Used by Hadza Foragers of Tanzania. *Journal of Food Composition and Analysis* 14: 15-25.

Sear, R. and R. Mace (2008) Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior* 29: 1-18.

Sear, R., R. Mace, and I.A. McGregor (2000) Maternal grandmothers improve nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society London Series B* 267: 1641-1647

Sear, R., F. Steel, I. Mc Gregor, and R. Mace (2002) The effects of kin on child mortality in rural Gambia. *Demography* 39: 43-63.

Smith, B.H. (1991) Dental development and the evolution of life history in Hominidae. *American Journal of Physical Anthropology* 86: 157-174.

Smith, B.H. (1992) Life history and the evolution of human maturation. Evolutionary Anthropology 1: 134-142.

Stearns, S. (1992) *The Evolution of Life Histories*. Oxford: Oxford University Press.

Strickland, J.D.H. and T.R. Parsons (1972) *A practical handbook of seawater analysis*. Ottawa: Fisheries Board of Canada.

Sugiyama, Y. (2004) Demographic parameters and the life history of chimpanzees at Bossou, Guinea. *American Journal of Physical Anthropology* 124: 154-165.

Trivers, R.L. (1977) The Evolution of Reciprocal Altruism. The Quarterly Review of Biology 46(1): 35-57.

Tronick, E.Z., G.A. Morelli, and S. Winn (1987) Multiple caretaking of Efe (pygmy) infants. *American Anthropologist* 89: 96-106.

Tucker, B. and A.G. Young (2005) Growing up Mikea: Children's time allocation and tuber foraging in the southwestern Madagascar. In *Hunter-Gatherer Childhoods, B. Hewlett and M. Lamb*, eds. Pp. 147-171. Aldine de Gruyter: New York.

Tukey, J.W. (1977) Exploratory Data Analysis. Reading, MA: Addison-Wesley.

Turke, P. (1998) "Helpers at the Nest": Childcare networks on the Ifaulk. In: *Human Reproductive Behaviour: A Darwinian Perspective*, L. Betzig, M. Borgerhoff-Mulder, and P. Turke, eds. Pp. 173-188. Cambridge: Cambridge University Press.

U.S. Department of Agriculture, Agricultural Research Service USDA National Nutrient Database for Standard Reference (2008) Release 21. Nutrient Data Laboratory Home Page. http:// www.ars. usda.gov/ba/bhnrc/ndl.

Van Beek, A.G. (1987) *The way of all pulp: Hunting and ideology of the Bedamuni of the Great Papual Plateau (Papua New Guinea)*. PhD Dissertation, University of Leiden, The Netherlands.

Van Soest, P.J. (1994) *Nutritional Ecology of the Ruminant*. Ithaca: Cornell University Press.

Vincent, A. (1984) Wild tubers as a harvestable resource in the East African Savannas: ecological and ethnographic studies. PhD Thesis, University of California, Berkeley, CA.

Vincent, A. (1985) Plant Foods in Savanna Environments: A Preliminary Report of Tubers Eaten by the Hadza of Northern Tanzania. *World Archaeology* 17(2): 131-148.

Voland, E. and J. Beise (2002) Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhorn. *Behavioral Ecology and Sociobiology* 52: 435-443.

Walker, R., M. Gurven, K. Hill, A. Migliano, N. Chagnon, R. De Souza, G. Djurovic, R. Hames, A.M. Hurtado, H. Kaplan, K. Kramer, W.J. Oliver, C. Valeggia, and T. Yamauchi (2006) Growth rates and life histories in twenty-two small-scale societies. American Journal of Human Biology 18: 295-311.

Wallis, J. (1997) A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility* 109: 297-307.

Wall-Scheffler, C.M., K. Geiger, K.L. Steudel-Numbers (2007) Infant Carrying: The Role of Increased Locomotory Costs in Early Tool Development. American Journal of Physical Anthropology 133: 841-846.

Watanabe, H. (1975) *Bow and arrow census in a West Papuan lowland community: A new field for functional-ecological study*. St. Lucia: Anthropology Museum, University of Queensland.

Weisner, T.S. and Ronald Gallimore (1977) My Brother's Keeper: Child and Sibling Caretaking. *Current Anthropology* 18(2): 169-190.

Werner, E.E. (1984) *Child care: Kith, Kin, and Hired Hands.* Baltimore: University Park Press.

Whiting, B.B. and J.W.M. (1975) *Children of six cultures: a psycho-cultural analysis*. Cambridge, MA: Harvard University Press.

Wich, S.A., S.S. Utami-Atmoko, T. Mitra Setia, H.D. Rijksen, C. Schurmann, J.A.R.A.M. van Hoof, and C.P. van Schaik (2004) Life history of wild Sumatran orangutans (*Pongo abelii*). Journal of Human Evolution 47(6): 385-398.

Wilson, E.O. (1971) *The Insect Societies*. Cambridge: Harvard University Press.

Woodburn, J. (1968) Stability and flexibility in Hadza residential groupings. In *Man the Hunter*, R.B. Lee and I. DeVore, eds. Pp. 103-110. Chicago: Aldine.

Woolfenden, G.E., and J.W. Fitzpatrick (1984) *The Florida scrub jay: demography of a cooperative-breeding bird*. Princeton, New Jersey: Princeton University Press.

Wrangham, R.W., J.H. Jones, G. Laden, D. Pilbeam, and N.L. Conklin-Brittain (1999) The raw and the stolen: cooking and the ecology of human origins. *Current Anthropology* 40: 567-594.

Wright, J. (1997) Helping-at-the-nest in Arabian babblers: signaling social status or sensible investment in chicks? *Animal Behaviour* 54 (6): 1439-1448.

Zellar, A.C. (1987) A role for children in hominid evolution. *Man* 22(3): 528-557.