

*Original Research Article***Cooperative Breeding and Maternal Energy Expenditure Among Aka Foragers**

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**Objectives:** Previous research among foragers and theory suggests that nonmaternal caregivers offer essential assistance, which supports female reproduction and the costs associated with lengthy child development. Mothers' face trade-offs in energy allocation between work and childcare, particularly when mothers have an infant. These trade-offs likely have crucial impacts on the pace of reproduction and child health. Caregivers can help mothers with childcare or they can reduce a mother's nonchildcare workload. If caregivers assist mothers by substituting childcare, then maternal energy expenditure (EE) in other work activities should increase. If caregivers assist mothers by substituting labor, then maternal EE in work activities should decrease when caregivers are present.

**Methods:** Utilizing detailed, quantitative behavioral observations and EE data, we test these propositions with data from 28 Aka forager mothers with children <35 months old. We isolate paternal, grandmaternal, and other caregiver effects on maternal EE and childcare in multivariate analyses.

**Results:** Our results show that caregivers (largely grandmothers) significantly reduce mothers' work EE by as much 216 kcal across a 9-hour observation period, while fathers and juveniles appear to increase maternal EE. Direct childcare from grandmothers decreases maternal direct care by about one-to-one indicating a labor substitution. Direct childcare from fathers decreases maternal care by almost 4 to 1, resulting in a net reduction of total direct care from all caregivers.

**Conclusions:** Our results indicate that there are multiple pathways by which helpers offset maternal work/childcare trade-offs. *Am. J. Hum. Biol.* 25:42–57, 2013. © 2012 Wiley Periodicals, Inc.

Human ontogeny requires that mothers invest heavily in their offspring (Blurton Jones and Marlowe, 2002; Hrdy, 2009), both calorically (Kaplan, 1994) and through caregiving (Hewlett and Lamb, 2002; Hrdy, 2009). Human children, born highly altricial, also remain dependent for an extended period (Bogin, 1999). Women have short interbirth intervals, high fertility, and simultaneously care for multiple dependent offspring (Kramer, 2010). Women also face competing demands on their energy allocation, particularly between childcare and subsistence/labor activities, with the height of this trade-off occurring during lactation (Gurven and Kaplan, 2006; Hawkes et al., 1997; Hill and Kaplan, 1988; Ivey, 2000; Peacock, 1985; Piperata, 2008).

Efe (Ivey, 2000) and Hadza (Hawkes et al., 1998) foragers demonstrate a negative association between time allocated to childcare and subsistence activities. Additionally, Aka forager mothers hold their infants approximately 50% less often during work activities than during leisure times (Meehan, 2009), suggesting that even among foragers who often carry their infants during subsistence tasks, work activities are not always compatible with childcare. Research suggests that mothers manage the childcare/labor trade-off by generally reducing their time allocated toward subsistence and other labor activities, rather than reducing infant care (Bove et al., 2002; Hurtado et al., 1992; Kramer, 2005, 2010; Marlowe, 2003). Cross-culturally, infants and younger children are especially vulnerable to poor environments and fluctuations in caregiving (Panter-Brick, 1998). Harsh environments, furthermore, during infancy appear to canalize human reproductive development, reducing phenotypic plasticity in adulthood (Quinlan, 2010), making reductions in caregiving to infants and young children risky. However, if mothers alter their strategy during the lactational state away from subsistence activities and toward infant care (Kramer,

2010), the effects of reduced labor may be associated with increased risk to mothers and older children (Hawkes et al., 1998; Piperata, 2008).

However, human and non-human primate nonmaternal caregivers can alter maternal strategies by assisting with childcare and provisioning during sensitive periods. Assistance may enable mothers to invest more energy in direct caregiving, or by offering direct childcare, enable mothers to reduce time allocated to childcare and increase labor activities. If nonmaternal caregivers provision mothers and young children, mothers can remain close to home (Gurven and Kaplan, 2006) or favor activities that do not jeopardize their caregiving (Hurtado et al., 1992). Hadza women reduce foraging when they have a new infant and the reduction, unless supplemented, can negatively affect child nutritional status (Hawkes et al., 1997). However, fathers and grandmothers buffer risk during these critical periods by provisioning mothers and children (Hawkes et al., 1998; Marlowe, 2003). These nutritional subsidies likely enable mothers to spend more time in direct childcare. Alternatively, when high-quality allomaternal care is available, costs associated with reducing childcare could diminish and mothers may spend more time in subsistence/economic activities (Bove et al., 2002; Mitani and

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Watts, 1997). Among the Efe, the number of caregivers is positively related to time mothers spent away from camp acquiring food, without the dual demand of childcare (Ivey Henry et al., 2005).

It is important to note that childcare/labor trade-offs during lactation are not isolated events during women's reproductive careers. Ethnographic descriptions illustrate that forager mothers often wean their children during subsequent pregnancies (Fouts et al., 2005). While there is variability in average recorded interbirth intervals among foragers [e.g., Ache 3.2 years (Hill and Kaplan, 1988); Aka 3.5 years (Hewlett, 1991); !Kung 4.0 years (Konner, 2005)], forager women are rarely not lactating during their reproductive stage. Consequently, the ways lactating women mitigate risks associated with a work/childcare trade-off are of particular importance for human life history.

#### *Human cooperative breeding*

The highly dependent nature of human children, unique human female life history traits, and work/childcare trade-offs suggest that cooperation in child rearing was an essential component to human fitness in our evolutionary history (Crittenden and Marlowe, 2008; Hrdy, 2009; Kramer, 2005, 2010). Without the assistance of others, it would be unlikely that human mothers could successfully meet the demands of multiple dependents simultaneously. Cooperative breeding—broadly defined as caregiving and provisioning by others—is predicted to buffer maternal work/childcare trade-offs, enabling women to produce more costly, more dependent, and more closely spaced offspring than they would be able to sustain on their own (Hrdy, 2009; Kramer, 2005, 2010).

Humans display the hallmarks of a cooperative breeding species—the reliance on allomaternal investment, cooperative group structures, and philopatry (Hrdy, 2005). Furthermore, the cooperative nature of child rearing is documented cross-culturally (Crittenden and Marlowe, 2008; Gottlieb, 2004; Ivey Henry et al., 2005; Konner, 2005; Lancy, 2008; Meehan, 2005; Tronick et al., 1992). Allomaternal investment is associated with positive outcomes in terms of child health and survivorship (Beise, 2005; Euler and Weitzel, 1996; Hawkes et al., 1997; Leonetti et al., 2005; Sear and Mace, 2008; Sear et al., 2002), child stress responses (Flinn and Leone, 2009), increased maternal responsiveness (Hrdy, 2007; Olds et al., 2002), and higher maternal fertility (Crognier et al., 2002; Kramer, 2005; Turke, 1988). Human cooperation, evident through widespread sharing of labor, food, and childcare (Hill et al., 2011), is crucial to understanding our demographic success as a species (Kramer, 2010).

#### *Maternal energy expenditure and nonmaternal care*

While time allocation studies have been particularly fruitful in investigating the effects of nonmaternal caregivers on maternal work/child trade-offs, there is increasing (e.g., Kramer et al., 2009; Madimenos et al., 2011; Panter-Brick, 2002; Piperata and Dufour, 2007; Piperata, 2008, 2009; Pontzer et al., 2012), albeit still limited, attention to the effects of this trade-off on female energetics. Biocultural energetic studies offer an avenue to consider the contexts and consequences of energy allocation

trade-offs on human survival and reproduction (Leonard, 2004, 2012; Snodgrass, 2012). All organisms face trade-offs in energy expenditure (EE) toward maintenance (resting/activity costs) and productive (growth/maturation/reproductive) costs (Chisholm, 1993; Kramer et al., 2009; Leonard, 2012; Stearns, 1992); however, it is difficult to investigate these trade-offs with time allocation data. Time allocation toward broadly defined work activities may not equate to high EE. In addition, recent energetic studies offer a means to explore how trade-offs in females' EE strategies are constrained and supplemented by others during vulnerable periods (i.e., growth, pregnancy, and lactation). As outlined below, these contributions point to human sociality and cooperation as a key component to female EE and emphasize that human energy allocation strategies are made within a particularly complex web of social, cultural, and ecological circumstances.

Energy for reproduction in most mammals is dependent upon the mothers' production, although in humans and other cooperative breeders, assistance through shared labor and childcare mitigates maternal costs—mothers are not solely reliant upon their own ability to garner energy for reproduction (Kramer, 2010). Nonmaternal investment, through pooled energy, shared resources, labor, and childcare tasks, has been associated with fast human life histories and high fertility (Kramer et al., 2009). As Kramer et al. note there is a paradox between fast human life histories and our understanding of energy budgets and allocation. Fast human life histories are associated with high extrinsic risk, yet under these conditions energy should be allocated toward immune function (McDade et al., 2008), suggesting that mechanisms that promote rapid maturation and early reproduction in humans were not well understood (Kramer et al., 2009). Kramer and colleagues (2009) study among the Pumé foragers suggests that human cooperation and pooled energy buffer girls' growth and development, and enable early reproduction.

Although results are somewhat mixed, evidence also suggests that cooperation continues to buffer women's energetic strategies and supports women's fecundity throughout their reproductive careers. Women in small-scale societies have fewer options for increasing nutritional intake during vulnerable periods and thus must balance energy during pregnancy and lactation through body fat stores obtained during pregnancy, or by reducing EE (Ellison, 2008; Guillermo-Tuazon et al., 1992; Panter-Brick, 1993; Piperata, 2008, 2009; Piperata and Dufour, 2007; Vinoy et al., 2000). However, the reduction in EE can have serious consequences unless others buffer that reduction. Piperata and Dufour (2007) showed that Ribeirinha, horticultural, Amazonian women decreased physical activity early postpartum as an energetic strategy. The Ribeirinha consider early postpartum a vulnerable period for new mothers and, in principle, labor restrictions should increase the amount of energy available for mothers to invest in their newborns. During *resguardo*, the 40-day period postpartum, husbands and others have obligations to increase their social and nutritional assistance to new mothers. However, Piperata and Dufour found that women in early postpartum were further from energy balance than women outside the restricted period. Despite adequate protein contributions from husbands, the lack of energy balance was associated with absence of

a primary food producer (the mother), resulting in a strain on household energy availability. Nevertheless, social support networks showed evidence of mitigating the effects. Women with social support networks came closer to energy balance during *resguardo* and peak lactation, and lost less weight (Piperata, 2009). In contrast, Shuar women maintain their base activity levels—women's increased needs are not met through their own reduction in EE. Rather, increase in family members', particularly spouses, economic contributions buffer maternal needs (Madimenos et al., 2011).

#### *Socioecology and cooperative breeding: Who helps?*

Studies investigating the effects of cooperative breeding have emphasized select nonmaternal caregivers, namely fathers and grandmothers (for exceptions see Crittenden and Marlowe, 2008; Ivey Henry et al., 2005; Mace and Sear, 2005; Marlowe, 2005; Meehan, 2005, 2009; Sear and Mace, 2009). Siblings have also proved to be an important category of nonmaternal caregivers; although much attention has focused on their caregiving investment (e.g., Hames, 1988; Meehan and Hawks, n.d.; Weisner and Galimore, 1977) over their economic contributions (Kramer, 2005).

While grandmothers, fathers, and siblings have continually been shown to support women's reproduction, nonmaternal caregivers are not limited to these individuals; caregivers encompass a range of categories (e.g., males/females, adults/juveniles, kin/non-kin). These caregivers have different motivations, skills, strengths, and goals (Hrdy, 2009; Ivey, 2000). Thus, we should expect that categories of nonmaternal caregivers will differ in their investment strategies and affect mothers and children in unique ways (Hurtado et al., 1992; Kramer, 2010; Sear and Mace, 2009). For instance, Hiwi and Ache women work fewer hours when their husband has high food returns—high paternal provisioning may enable mothers to spend more time in direct childcare. Yet, the number of dependents a woman has is positively associated with her foraging returns (Hurtado et al., 1992). As a woman's total fertility increases, she must provide for growing numbers of dependent children. Under this circumstance, it is possible that Hiwi and Ache mothers risk the reduction in direct caregiving to infants to engage in subsistence activities for the benefit of their older children. It is also possible that, particularly among the Hiwi, alloparents enable mothers to spend more time in subsistence activities and increase their foraging returns (Hurtado et al., 1992). Alternatively, Kramer's (2005) research among Maya found that juveniles' investment in economic activities, over caregiving, helps offset the cost of maternal reproduction—juveniles contribute to their own and sibling nutritional needs. While subsistence strategies certainly play a role in who is capable of assisting, Kramer cautions that variation may not necessarily be associated with modes of subsistence—forager children show tremendous cross-cultural variation in time devoted toward food production and domestic tasks (Kramer, 2010). Cross-cultural variation in who helps and the pathways by which help is distributed suggests there is much work to be done to tease apart the effects of socioecology on women's energetics in diverse social and physical environments. If we are to link the dependent nature of human children and their need for nonmaternal care to the evolution of human

social behavior and human life history traits, it is necessary to document children's complete social environments and the potentially different ways in which nonmaternal helpers affect maternal energy allocation strategies across varied ecologies.

Here we examine how cooperative breeding and camp composition affect maternal EE and parental investment strategies. We take a biocultural approach to investigating Aka women's strategies by integrating multiple lines of data: (1) detailed maternal behavioral observations, which offer contextual information on women's activity patterns; (2) factorial EE data, which allow us to capture EE across multiple types of women's activities; (3) child and caregiver behavioral observations, which enable us to explore the frequency of care children receive across caregiver categories; and (4) demographic and social data, which allow us to investigate how women's strategies are situated in and affected by our prosocial nature.

We first describe Aka maternal EE and socioecology. We then investigate the effect of maternal socioecology on Aka mothers' EE, exploring the role of fathers, grandmothers and the full range of other alloparents. We examine how particular categories of allocaregivers differentially affect EE strategies and maternal childcare time allocation. We expect that alloparents who act as substitutes for maternal, nonchildcare work decrease maternal work EE, and alloparents who substitute direct childcare increase maternal work EE. This integrative approach enables us to take a small step toward untangling the myriad of biological, behavioral, and social influences on human female energy trade-offs.

#### STUDY POPULATION

The focal Aka population are mobile tropical forest foragers located in southwest C.A.R. The Aka share a common ancestry with other foraging populations in western and central Africa (Quintana-Murci et al., 2008), perhaps as recently as 3,000 years ago (Verdu et al., 2009), yet tropical forest foragers display tremendous linguistic and cultural diversity (Bahuchet, 1985; Berry et al., 1986; Hewlett, 1996). The Aka hunt and gather forest game, insects, honey, and numerous plant species for subsistence (Hewlett, 1991). Individuals spend a portion of each year living on the rainforest periphery in camps near settled farming communities. While near villages, Aka men and women work in their neighbors' fields. As with all Central African forest foragers, their association with the farmers enables access a variety of domesticated plants, which constitutes a significant portion of their diet (Bahuchet, 1988).

Similar to other foraging populations in the region (Fouts et al., 2005), the Aka emphasize egalitarianism and sharing. With few exceptions, food items are shared widely among camp members. Extensive sharing is expected considering the high level of cooperation needed between individuals participating in a foraging lifestyle (Hewlett, 1991), and an extension of this sharing pattern can be seen in childcare during infancy and early childhood.

Early infancy is characterized by intense caregiving—children breastfeed on demand and sleep with their parents, enabling continuous night-time breastfeeding. At 3–4 months children are held over 90% of the day (Hewlett et al., 2000) and in late infancy, children are held almost 60% of day (Meehan, 2005). Young children often

travel with their mothers and others during daily activities and thus have frequent opportunities to be cared for by a variety of individuals throughout the day (Meehan, 2005).

Allomaternal care, direct care and provisioning, is extensive. Aka children have approximately 20 caregivers each day, 10 of whom offer intensive forms of caregiving (holding, feeding, bathing, etc.) (Meehan, 2009; Meehan and Hawks, n.d.). Nonmaternal care is undertaken by multiple individuals who span age, sex, and relationship categories (Meehan, 2005). Fathers and grandmothers offer the second and third highest frequency of direct care to infants, with mothers being children's primary caregivers. However, the sum of all other nonmaternal caregivers' (siblings, other adults, other juveniles), exceeds the frequency of paternal and grandmaternal care (Meehan, 2008a). Caregivers are highly responsive, sensitive, and are responsible for approximately one-quarter of all childcare in daylight hours (Meehan, 2008a; Meehan and Hawks, n.d.). Unfortunately, environmental risk is high—infant mortality is approximately 20% (Hewlett, 1991) and child mortality is over 35%, with infectious and parasitic diseases the primary cause of infant and child mortality (Hewlett et al., 2000).

#### METHODS AND DATA

Data were collected over two field seasons in the Central African Republic. The first (June–early July 2009) occurred during the wet season, but prior to the start of the heaviest rains which peak in August (Bahuchet 1988; Hewlett 1991). The second (January–February 2010) occurred during the dry season. While there is variation in rainfall, there is minimal temperature fluctuation during the year—the range in mean monthly temperature is only 23.4–25.8°C (Bahuchet, 1988). As is common (Bahuchet, 1988), many of the Aka were working for the neighboring horticultural farmers, the Ngandu, during the dry season. There was also a high density of families close to the village in June and July. The Aka reported that they were helping the Ngandu in their fields to prepare for both Aka and Ngandu extended departures to the forest once the caterpillar season commenced in August.

##### *Maternal observation procedure*

Naturalistic behavioral observations were conducted on mothers using a focal individual sampling strategy (Altmann, 1974). This observation procedure has been used successfully in numerous child studies in recent years (e.g., Fouts et al., 2005; Hewlett et al., 2000; Meehan, 2005, 2008b, 2009). The procedure required the researchers to observe and follow a focal individual over several days covering all daylight hours (6 am–6 pm). Maternal observations occurred in 4-hour intervals from 6 am–10 am, 10 am–2 pm, and 2 pm–6 pm. The 4-hour observations were spread over multiple days to capture the variation in the mothers' daily activities. Each 4-hour observation segment starts at the top of an hour and continues for 45 minutes. At the end of 45 minutes, the observer takes a 15-minute break (e.g., observe and record from 6:00:00 am–6:44:59 am and break from 6:45:00 am–6:59:59 am, observe and record from 7:00:00 am–7:44:59 am, etc.). Due to the 15-minute break following every 45 minutes of observations, mothers were actually observed for 9 of the

12 daylight hours. Tape recorders with an earphone were carried that directed the observer to observe starting at the top of the minute, record on handheld data sheets during 0:00:20–29 seconds, resume observation at 0:00:30 seconds, record during 0:00:50–59 seconds, etc. Thus, observation units are 30-seconds, resulting in 1,080 observations per focal mother, or 30,240 intervals for the sample. In total, mothers were observed for 252 hours. Observations generally occurred over a 3-day period, although 3 of the 28 women's observations occurred over a 2-day period. However, even for these women observation segments were not sequential. Observations were conducted during daylight hours due to the difficulty of collecting observational data after dark. Aka women spend most evening hours in low-energy leisure activities, which would not likely significantly increase working EE.

Predefined maternal labor categories were coded: *walking with no load*; *walking with a light load* (<10 kg); *walking with a heavy load* (10–35 kg); *collecting water* (actively gathering water); *collecting firewood* (chopping with an ax or breaking wood apart by hand); *food processing* (pounding, grinding, or chopping food); *cooking* (actively tending, stirring, manipulating food on an open fire); *cleaning* (sweeping or picking up inside the hut or around camp); *construction or repair* (building huts, making baskets, repairing tools, etc.); *foraging* (active collection of food resources – not passive scanning); *fieldwork* (weeding, clearing, or harvesting crops in farmers' fields); *sleep* (eyes closed, laying down, slowed breathing); and *leisure* (at rest and not participating in any of the activities above). Load weights during travel were estimated on the spot. Weighing mothers' baskets, containers, or items carried in their arms would be disruptive, particularly during naturalistic observations, designed to minimize the effect of the observer on participant behavior. Baskets containing bundled leaves, small water containers, or one or two small logs were easily estimated at <10 kg, *light load*. *Heavy loads* were defined more broadly and included large baskets of firewood, containers filled with manioc tubers, or large water containers.

##### *Child observation procedure*

Separate child focal observations, focused on child behaviors and child-caregiver interactions were conducted on focal mothers' children (<35 months). The methodology is identical to the maternal observations. Children were observed over several days; yet, the observations spanned all daylight hours (6 am–6 pm). Again, due to 15 minute breaks following every 45 minutes of observations, child and caregiver behavior was observed for 9 out of the approximately 12 daylight hours in the region. Child behavior and child-caregiver interactions were recorded 1,080 times per child or 30,240 times for the entire sample. In total, focal children were also observed, albeit during separate observations, for 252 hours.

Children's caregivers were identified during the child observations. Prior to commencing the observations, each individual in camp was given a unique identifier. A caregiver's code was then recorded each time the individual interacted with the focal child during the observations. Additional unique identifiers were assigned on the spot if a child interacted with a noncamp member. Identifying individuals and their interactions with children enable analysis of social/caregiver network size and variation in

sex and kinship relations between the focal child and his or her caregivers.

Observers were trained in the methodology in the United States at local daycare centers prior to departing for the C.A.R. Observers met interobserver reliability at  $\geq 90\%$  for all behavioral categories discussed with the exception of proximity and vocalization, for which inter-reliability scores were  $\geq 80\%$ .

Aka children live in nested social networks. Due to the small size of Aka camps, children experience at least some form of visual or audio contact with all camp members (their social network) on a daily basis. They have a smaller number of individuals (their caregiving network) who offer direct or passive forms of childcare to them. As mentioned above, approximately half of the caregiving network engages in intensive forms of investment (their high-investment network). These caregivers hold, soothe, offer medical or hygienic care, feed, nurse, play with, or direct affectionate behaviors toward the child. Children also have an even smaller unit of caregivers (their attachment network) to whom they purposefully seek out and/or direct attachment behaviors toward (Meehan and Hawks 2011, n.d.).

While children see or hear camp members daily, not all camp members come into proximity, engage, or invest in children (Meehan, 2009), thus their social network (the number of individuals in a camp) does not represent their caregiving network. The high-investing category highlights who offers the most intensive forms of investment, but significantly underestimates the number of individuals who participate in childcare on a daily basis. Focusing only on high-investing caregivers eliminates any caregiver who engages in passive childcare (watching, checking, touching, physical proximity, etc.), even if this caregiver was clearly a child's minder during a maternal absence. For example, if a child and caregiver simply have physical contact, achieved through touching, the caregiver is not considered a high-investing caregiver. We consider touching to be passive because while touching may be an intentional action on the part of a caregiver, a caregiver does not necessarily need to direct their attention toward an infant or child to maintain physical contact. We also consider proximity, conservatively defined as within a forearm's distance to the focal child, to be under the umbrella of passive childcare. Proximity, by itself, does not entail any effort expenditure; yet individuals who are within a forearm's distance are caregivers who are attentive to children's behaviors and those who respond to children needs (Meehan, 2005). Individuals who participate in both direct and passive forms of childcare contribute to children's safety and security and passive caregivers serve a greater role as children age and spend less time held.

Mothers and fathers discussed in the analysis are the putative genetic parents of the focal children. Adult females and males are those who are married, have children, or who are beyond 18 years old. Juveniles are camp members between 4 to 18 years old. The Aka consider children at 4–6 years of age (*kombèti*) to have "good sense" and to be capable of helping with childcare (Helfrecht, 2012). Individuals under four are not considered alloparents. While we have observed 3-year olds interacting with and engaged in multiple forms of childcare (e.g., holding, cleaning the child, feeding, touching and proximity), these caregivers are never left alone with children. Additionally, due to the size, strength, competence level and difficulty

of determining motivation in a 3-year old caregiver, they have been eliminated from the analysis.

#### Calculating maternal EE

EE was calculated using mothers' estimated basal metabolic rates (BMR) and physical activity ratios (PAR), as described in Snodgrass (2012) and Ulijaszek (1995). Aka mothers' BMRs were calculated using equations from FAO/WHO/UNU (1985) based on maternal age, weight, and height. The use of predictive equations for BMR has proven to be accurate within 10% of directly measured values (Dufour and Piperata, 2008). The Aka do not keep track of birth dates. However, based on the average age at first marriage and age at first birth (Hewlett, 1991), along with data on maternal reproductive histories which documented focal mothers' number of children (both living and deceased), we were able to estimate maternal age ( $\pm 3$  years). As part of larger family health survey, maternal weight and height were collected immediately following the completion of the behavioral observations.

PAR values were obtained or calculated from studies among subsistence foraging and farming populations and developing and developed societies (Table 1). They were selected from available literature based on applicability to observed Aka women's labor activities and secondarily by similarity of climate and subsistence strategy. While values from available hunter-gatherer populations and many other subsistence level societies were used when available, the majority of the PAR values came from FAO/WHO/UNU (1985). FAO/WHO/UNU provides a large compilation of PAR values from developed and developing societies. It was necessary to utilize PAR values not derived from studies of tropical forest foragers as there is a dearth of research on human energetics on these populations, likely due to the difficulty operationalizing EE studies with mobile groups (for exceptions see: Madimenos et al., 2011; Pasquet and Koppert, 1993; Pontzer et al., 2012; Yamauchi et al. 2000). Furthermore, only a few studies of hunter-gatherers provide EE for specific activities (Montgomery and Johnson, 1977; Pasquet and Koppert, 1993). Hunter-gatherer and forager-horticulturalist studies often measure total energy expenditure (TEE) instead of EE during specific activities (Madimenos et al., 2011; Pontzer et al., 2012; Yamauchi et al., 2000). A compilation of PAR values from the current hunter-gatherer literature would not suffice in estimating EE for the wide variety of activities we observed the Aka participating in. For example, hunter-gatherer PAR values are available for many of the food processing activities observed among the Aka, but no PAR values exist for sharpening knives in preparation for food processing, sweeping the ground in camp, or repairing/building a hut (*huma*). These activities were frequently recorded during the maternal behavioral observations. Thus, to achieve an accurate estimate of women's EE, non-forager PAR values were utilized.

There may be differences in metabolic efficiency between foragers, horticulturalists, and Western subjects (Shea and Bailey, 1996). However, the use of height, weight, and age to calculate the BMR of each participant should minimize error in EE estimations when using PAR values from sources other than tropical forest foragers. In addition, although energetic studies are limited, available literature indicates no discernible differences between forager and Western energetics as they relate to our study.

TABLE 1. PAR references for EE variables

EE variable	PAR average (range <sup>a</sup> )	Subsistence pattern	Location	PAR values in mean	Methods <sup>b</sup>	Reference	
Sleep	0.97 (0.94–1.0)	Developed and developing societies	Nonspecific	1	1	FAO/WHO/UNU, 1985	
			Nonspecific	1	2	Garby et al., 1987	
Leisure	1.2	Developed and developing societies	Nonspecific	1	1	FAO/WHO/UNU, 1985	
Walking with no load	3.4 (1.8–6.6)	Subsistence agriculturalists	West Africa	1	1	Bleiberg et al., 1980	
			Horticulturalists	Amazon	3	1	Dufour, 1984
			Developed and developing societies	Nonspecific	8	3	FAO/WHO/UNU, 1985
			Subsistence farmers	New Guinea	11	1	Norgan et al., 1974
			Hunter–agriculturalists	Cameroon	1	1	Pasquet and Koppert, 1993
Walking with heavy load	3.75 (3.39–4.57)	Agriculturalists	Guatemala	2	1	Torun et al., 1982	
			Farmers	Tropical China	1	1	Brun, 1992
			Horticulturalists	Amazon	4	1	Dufour, 1984
			Hunter–agriculturalists	Cameroon	1	1	Pasquet and Koppert, 1993
Walking with light load	3.39	Agriculturalists	Guatemala	1	1	Torun et al., 1982	
Collect water	2.2	Developed and developing societies	Nonspecific	1	3	FAO/WHO/UNU, 1985	
Collect firewood	4.24 (3.52–4.91)	Developed and developing societies	Nonspecific	1	3	FAO/WHO/UNU, 1985	
			Hunter–agriculturalists	Cameroon	1	1	Pasquet and Koppert, 1993
			Agriculturalists	Guatemala	1	1	Torun et al., 1982
			Subsistence agriculturalists	West Africa	1	1	Bleiberg et al., 1980
Process food	2.66 (1.4–4.97)	Subsistence agriculturalists	Horticulturalists	Amazon	2	1	Dufour, 1984
			Developed and developing societies	Nonspecific	4	3	FAO/WHO/UNU, 1985
			Agriculturalists	Gambia	2	1	Lawrence et al., 1985
			Hunter–gatherer–horticulturalists	Peru	3	1	Montgomery and Johnson, 1977
			Subsistence farmers	New Guinea	1	1	Norgan et al., 1974
			Hunter–agriculturalists	Cameroon	3	1	Pasquet and Koppert, 1993
			Developed and developing societies	Nonspecific	2	3	FAO/WHO/UNU, 1985
			Subsistence farmers	New Guinea	1	1	Norgan et al., 1974
Cook	1.57 (1.2–1.99)	Agriculturalists	Guatemala	1	1	Torun et al., 1982	
			Subsistence agriculturalists	West Africa	1	1	Bleiberg et al., 1980
			Farmers	Tropical China	1	1	Brun, 1992
Clean	2.89 (1.7–3.76)	Developed and developing societies	Agriculturalists	Gambia	1	1	Lawrence et al., 1985
			Hunter–gatherer–horticulturalists	Peru	2	1	Montgomery and Johnson, 1977
			Subsistence farmers	New Guinea	1	1	Norgan et al., 1974
			Agriculturalists	Guatemala	3	1	Torun et al., 1982
			Developed and developing societies	Nonspecific	2	3	FAO/WHO/UNU, 1985
			Hunter–gatherer–horticulturalists	Peru	1	1	Montgomery and Johnson, 1977
			Subsistence farmers	New Guinea	4	1	Norgan et al., 1974
Construct or repair	1.5 (1.3–2.29)	Developed and developing societies	Nonspecific	2	3	FAO/WHO/UNU, 1985	
			Hunter–gatherer–horticulturalists	Peru	1	1	Montgomery and Johnson, 1977
			Subsistence farmers	New Guinea	4	1	Norgan et al., 1974
Forage	3.42 (1.7–5.44)	Farmers	Tropical China	1	1	Brun, 1992	
			Horticulturalists	Amazon	1	1	Dufour, 1984
			Developed and developing societies	Nonspecific	4	1	FAO/WHO/UNU, 1985
			Agriculturalists	Gambia	2	1	Lawrence et al., 1985
			Hunter–gatherer–horticulturalists	Peru	1	1	Montgomery and Johnson, 1977
			Subsistence farmers	New Guinea	4	1	Norgan et al., 1974
			Hunter–agriculturalists	Cameroon	1	1	Pasquet and Koppert, 1993
			Agriculturalists	Guatemala	3	1	Torun et al., 1982
Fieldwork	3.5 (1.5–5.44)	Subsistence agriculturalists	West Africa	2	1	Bleiberg et al., 1980	
			Farmers	Tropical China	1	1	Brun, 1992
			Horticulturalists	Amazon	2	1	Dufour, 1984
			Developed and developing societies	Nonspecific	10	3	FAO/WHO/UNU, 1985
			Agriculturalists	Gambia	2	1	Lawrence et al., 1985
			Hunter–gatherer–horticulturalists	Peru	3	1	Montgomery and Johnson, 1977
			Subsistence farmers	New Guinea	10	1	Norgan et al., 1974
			Hunter–agriculturalists	Cameroon	1	1	Pasquet and Koppert, 1993
			Agriculturalists	Guatemala	1	1	Torun et al., 1982

<sup>a</sup>Leisure, travel with light load and collect water do not have PAR ranges, because only one PAR value was used.

<sup>b</sup>1, indirect calorimetry; 2, direct calorimetry; 3, indirect and/or direct calorimetry.

Feretti et al.'s (1991) study among the Bakola and Minetti et al.'s (1994) among the Baka foragers found differences in the energy cost of running between foragers and Caucasian men, but similar energy costs for walking speeds. No Aka women were observed running during the observations. Pasquet and Koppert's (1993) study among Yassa (fishermen-agriculturalists) and Mvae (hunter-agriculturalists), both Cameroonian tropical forest populations, document that women's EE in subsistence activities were similar to other tropical forest populations. Furthermore, a study of TEE among the Baka of Cameroon found their

physical activity level (PAL = TEE/BMR) to be similar to other African groups (Yamauchi et al., 2000) and a recent study among the Hadza hunter-gatherers found TEE to be statistically indiscernible from that of Western subjects when controlling for body size (Pontzer et al., 2012). Utilizing height and weight in our calculations of BMR, and drawing on PAR values obtained from cross-cultural sources, but limited to those that closely align with Aka maternal work activities, creates the most accurate estimate of Aka EE.

For sources that did not provide PAR values, values were computed by isolating BMRs for study subjects using

the FAO/WHO/UNU prediction equations (see Vaz et al., 2005). Thus, PAR values for maternal time activities were created by finding the mean of all applicable PAR values found in the literature (Table 1). No PAR values were used that were derived from studies of men or of primarily pregnant women. EE was calculated based on the mean of all relevant PAR values from the literature.

EE estimates are focused on nonchildcare activities. Unfortunately, no available studies offer EE estimates on childcare beyond added weight through carrying. We did not estimate holding EE because all but one of the focal children in this study weighed less than 10 kg (defined as traveling with a light load) and that traveling with no load and traveling with a light load have similar EE costs. We feel strongly that EE studies will benefit by investigating EE in childcare activities, which could be accomplished through the use of accelerometers, but current EE childcare estimates do not exist.

Participants were lactating at the time of the observations. Although BMR has been shown to increase for lactating women (Prentice et al., 1996), several studies indicate that lactation does not significantly affect BMR (Goldberg et al., 1991; Guillermo-Tuazon et al., 1992; Illingsworth et al., 1986; Schutz et al., 1980; Singh et al., 1989). A recent study measuring TEE with the Hadza using the doubly labeled water method found EE for lactating women to be no different than nonlactating (Pontzer et al., 2012). However, this could be due to a reduction in work activities postpartum as opposed to a negligible energy cost for lactation. Butte and King (2005) calculated the energy cost of lactation to range between 1.92–2.16 MJ/day for partially breastfeeding women in developing countries, depending on number of months postpartum (0–24). FAO/WHO/UNU (2004) estimate an average cost of 675 kcal/day for exclusive breastfeeding during the first 6 months, and 460 kcal/day for partial breastfeeding after 6 months. Here, focal children's ages range from 1 month to almost 3 years and Aka children begin receiving complementary feedings (water and/or food) within the first few days of life (Wilcox Roulette and Meehan, 2012). As child age, milk volume production, and the level of complementary feeding affect lactation energy cost (Butte and King, 2005), accurately calculating EE for breastfeeding Aka women is not possible with our current dataset. Thus, our focus is centered on EE during labor activities.

Multiple studies have estimated EE using the factorial method (time allocation) based on measured EE from external sources (Hill et al., 1984; Leonard and Robertson, 1992; Piperata and Dufour, 2007; Sackett, 1996). We recognize that calculating EE from behavioral observation, such as those described above, has not been fully evaluated (Dufour and Piperata, 2008); however, Snodgrass (2012) and Westerterp (2009) have noted that all methods for estimating EE and physical activity level have clear advantages and disadvantages. Behavioral observations offer the unique advantage of detailed contextual information, but reported disadvantages include high observer time/cost, the potential for subjective data, and high degrees of subject interference during behavioral observations. To ensure objective data collection, the lead author developed and trained additional data collectors on predefined labor activities. Activity categories were chosen by the lead author after hundreds of hours of direct observation of Aka women's daily lives and activity schedules.

Additionally, Aka participants are accustomed to the researchers' presence and conduct their daily activities with minimal modification (Hewlett et al., 2000). Furthermore, EE studies in general rely on PAR values measured at different times of the day, altitudes, climates, all of which affect EE (Ulijaszek, 1995). We argue that the frequency of our maternal behavioral observations (1,080 per focal mother), the fact that observations were collected at 30-second intervals across all daylight hours, and that the three, 4-hour observations segments were collected over several days, creates a robust data set yielding high resolution maternal time allocation estimates. From these data we gain valid estimates of maternal EE.

### Analysis strategy

We used an "ethnographic cone" analysis strategy adapted for quantitative analysis from Agar (1996). The procedure is to move from general raw field data based in participant observation, interviews and formal direct observation to a theoretically informed and empirically grounded analysis of alloparental effects on Aka mothers' EE. The challenge here is to explore the structure of this small sample realistically, appropriately and parsimoniously. We begin by reducing EE and Aka camp variables using principal components analysis (PCA). These PCAs give insight into the underlying structure of these data, suggesting appropriate scale construction and control variables for multivariate hypothesis driven models. Given the very small sample and the relatively large number of variables, we pay special attention to model adequacy and stability throughout the analyses. One target criteria for ideal model stability is  $n/k \geq 10$  where  $n$ =sample size, and  $k$ =predictor variables in a regression model. Given our sample of 28, we are only able to achieve  $n/k = 9.3$  with three predictors or control variables. Our modeling of similar ethnographic data (unpublished) indicates that small sample results from high resolution data remain stable with  $n/k > 5$ . Regardless, we are sensitive to model stability and we provide evidence of it throughout the analyses. We used bias-corrected accelerated bootstrapping with 1,000 replications for all  $P$ -values presented. We set alpha at 0.05 for considering significant main effects. We set alpha at 0.10 for retaining control variables in the models.

This research was reviewed and approved by the Washington State University Institutional Review Board. Informed consent was obtained by verbal consent in the presence of a research team member and a local field assistant who served as a witness to the verbal consent procedure.

## RESULTS

### Sample description

The total sample consists of 28 focal mothers and children. The average age of the focal mothers was 27.9 years (min = 19, max = 42, sd = 6.53). Not atypical to the larger population, the majority of focal mothers reported a history of health problems associated with parasites, pain from labor activities, and two women reported recent bouts of mastitis. However, maternal self health reports and observers' reports at the time of observation ranged from average to good health. The age distribution of the focal children was: seven children 1–<6 months; five

TABLE 2. Descriptive statistics for Aka mothers' nonchild care energy expenditure<sup>a, b</sup>

EE variable	Kcal mean (% of time in activity) <sup>c</sup>	Std. dev.	Min	Max
Sleep	2.4 (<0.01)	7.1	0.0	30.1
Leisure	316.1 (0.64)	85.6	146.6	492.0
Walking with no load <sup>d</sup>	63.0 (0.05)	40.9	0.0	167.2
Walking with heavy load <sup>d</sup>	44.9 (0.03)	50.1	0.0	161.3
Walking with light load <sup>d</sup>	27.8 (0.02)	40.8	0.0	165.0
Collect water	3.3 (<0.01)	4.8	0.0	19.7
Collect firewood	17.3 (<0.01)	24.3	0.0	84.3
Process food	123.3 (0.11)	86.6	7.8	351.1
Cook	13.3 (0.02)	9.9	0.0	42.9
Clean	37.9 (0.03)	26.7	1.1	86.1
Construct or repair	17.8 (0.03)	29.3	0.0	155.5
Forage	7.8 (<0.01)	14.7	0.0	52.9
Fieldwork	90.7 (0.06)	123.6	0.0	373.5
Total EE	765.6			

<sup>a</sup>Energy expenditure refers to estimated energy expenditure over the 9 h of observation.

<sup>b</sup>N = 28.

<sup>c</sup>Mean percentage of time participants engaged in an activity over the 9-h observation period.

<sup>d</sup>Load weights for carrying children are not included. With the exception of one child, the focal children all weighed less than 10 kg, the upper limit for traveling light, suggesting that carrying an infant would not significantly change our EE estimates.

children 6–<12 months; nine children 12–<24 months; and seven children 24–32.75 months. Determining age for infants and young children is reliable, as mothers, fathers, and other caregivers have recent memory of the season or events which enabled us to pinpoint the child's birth month. To cross-check parental age estimates, relative aging to other children was also conducted. Approximately 43% of children did not have their father living in camp at the time of observations. Over 70% of the children had a maternal or paternal grandmother residing in the same camp, which is higher than previous estimates of the number of children with access to a grandmother (Meehan, 2005). It is important to note that over 75% of the women in this sample are <30 years, increasing the probability that a grandmother is still living (Hill and Hurtado, 2009). The average camp size was 26.3 individuals (min = 7, max = 38, sd = 8.78). On average children had 1.8 siblings residing in camp with them (min = 0, max = 5, sd = 1.63).

#### Data structure of maternal EE

Table 2 shows descriptive statistics for Aka mothers' EE and includes, for context, the percentage of time that mothers devoted to activities. As previously reported, Aka women spent the vast majority of time in leisure activities (64%) (cf. Hewlett et al., 2000; Meehan, 2009). Fieldwork comprised a relatively large component (6%) of women's time spent in labor activities, likely due to their proximity to the village. Time in the field is often dedicated toward weeding, digging, planting, and harvesting. Fieldwork activities are often a blocked unit of time and more continuous in nature than other activities—women rarely engage in other types of labor while in the fields. The percentage of time spent in active foraging was (<1%). This may seem lower than expected; however, this percentage does not represent the amount of time dedicated to a foraging excursion. Foraging excursions include traveling (coded as travel with no weight, travel light, and travel heavy). Additionally, foraging excursions are often inter-

TABLE 3. Unrotated first component of maternal EE<sup>a</sup>

Variable	Comp 1
Leisure	-0.40
Sleep	-0.19
Walking with no load	0.31
Walking with heavy load	0.38
Walking with light load	0.12
Collect water	0.43
Collect firewood	0.39
Process food	0.27
Cook	0.04
Clean	0.35
Construct or repair	0.02
Forage	0.09
Fieldwork	-0.08

<sup>a</sup>If total EE is a simple unidimensional, additive construct, then all or most of the 13 variables should load positively and substantially (>0.3) on the first unrotated component. Results in this table indicate that that is not the case.

mixed with water and firewood collection and at times food processing. Passive foraging, when women were out on a foraging excursion and scanning the environment for resources were not included because these activities do not require more EE than what we calculated under travel. Coding foraging when women stopped and visually scanned the landscape would overestimate EE toward foraging activities. Active foraging was only coded during collection times, underestimating the amount of time women spent in pursuit of foraged items, but offering an accurate estimate of the amount of energy devoted to foraging. Foraging activities observed during observations included wild yam, nut, termite, and plant collections. Much like foraging, domestic tasks (cooking, cleaning, and/or construction and repair activities) are often interspersed with other tasks. For example, time devoted to cooking is far greater than (2%), yet much of cooking is passive (e.g., waiting for water to boil) and is often spent in leisure activities. In sum, maternal EE and the corresponding percentage of time that women spent in activities is in reference to active and not passive participation in activities.

We conducted PCA on Aka maternal EE. We used PCA to explore the activity structure of Aka mother's EE, to suggest an appropriate EE scale and control variables for further analysis. First we submitted 13 EE variables for PCA. If total EE is a simple unidimensional, additive construct, then all or most of the 13 variables should load positively and substantially (>0.3) on the first unrotated component. Table 3 indicates that is not the case, suggesting we explore the activity structure of EE further.

Additional analysis showed five components with Eigenvalues greater than 1 (Table 4). Varimax rotation yielded interpretable components. Component 1 is largely characterized by a negative loading for leisure (-0.58), followed by positive loadings for walking with heavy load, collecting firewood, and fieldwork, with loadings strength in that order. Component 2 is characterized by positive loadings for cleaning (0.59) and collecting water (0.52), and negative loading for fieldwork. Component 3 shows two positive loadings for cooking (0.58), followed by a substantial positive loading for food processing (0.46), and a negative loading for walking with no weight (-0.57). Component 4 is strongly characterized by a positive loading for foraging (0.7), followed by a positive loading for walking with light load, and negative loading for construct or repair. Component 5 is strongly characterized by sleep (0.80), followed by a modest negative loading for walking with light load.



TABLE 4. Principal components analysis of energy expenditure variables among Aka mothers

Variable	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5
Eigen value	2.60	2.31	1.68	1.56	1.30
Cumulative variance	0.20	0.38	0.51	0.63	0.73
<b>Leisure EE</b>	<b>-0.58</b>	0.05	0.14	0.05	0.03
<b>Sleep EE</b>	-0.03	-0.03	-0.04	0.04	<b>0.80</b>
Walking with no load EE	0.21	0.26	<b>-0.57</b>	-0.14	0.07
Walking with heavy load EE	<b>0.47</b>	-0.05	0.14	0.22	-0.16
Walking with light load EE	-0.08	0.06	-0.13	<b>0.48</b>	<b>-0.38</b>
Collect water EE	0.11	<b>0.52</b>	-0.11	0.08	-0.03
Collect firewood EE	<b>0.41</b>	0.21	0.12	0.16	<b>0.31</b>
Process food EE	0.28	0.10	<b>0.46</b>	-0.13	-0.15
Cook EE	0.03	0.12	<b>0.58</b>	-0.12	0.08
Clean EE	0.00	<b>0.59</b>	-0.04	-0.17	-0.04
Construct or repair EE	0.13	-0.12	-0.12	<b>-0.32</b>	-0.21
Forage EE	0.07	-0.05	0.00	<b>0.70</b>	0.10
Fieldwork EE	<b>0.32</b>	<b>-0.47</b>	-0.16	-0.14	0.04

Note: Component loadings greater than |0.3| are indicated in bold, defining the components.

TABLE 5. Descriptive statistics Aka mothers' camp demography (N = 28)

Variable	Mean	Std. dev.	Min	Max
Grandmother	0.71	0.46	0	1
Father	0.57	0.50	0	1
Camp size	26.32	8.78	7	38
Number of adult males	5.36	2.00	1	8
Number of adult females	7.71	3.16	1	12
Adolescent males	0.82	0.86	0	2
Adolescent females	0.82	1.09	0	4
Males 0-14	5.79	2.25	1	10
Females 0-14	5.82	2.51	0	10
Number of brothers <5 years old	0.21	0.42	0	1
Number of brothers 5-10 years old	0.46	0.69	0	2
Number of brothers 11-18 years old	0.32	0.77	0	3
Number of sisters <5 years old	0.25	0.44	0	1
Number of sisters 5-10 years old	0.43	0.57	0	2
Number of sisters 11-18 years old	0.18	0.39	0	1
Number of nonmaternal caregivers	20.93	7.50	7	40
Number of high investing nonmaternal caregivers	9.61	3.99	4	19

There are trade-offs between resting and work in activity budgets that should inform our analysis. Sleep and leisure are two important aspects of BMR. The PCA shows that any scale we develop needs to be chosen with due consideration for sleeping and leisure. We constructed a simple additive scale for maternal work EE by summing values of all EE estimates except for sleeping and leisure. This allows us to retain the original EE units (rather than factor scores) to develop predictive models of maternal working EE in kilocalories. We evaluated correlations among working EE, leisure and sleep. Leisure is strongly inversely associated with working EE (-0.86, they are opposite poles of the activity budget), while sleeping has a small inverse association with working EE (-0.23), suggesting that estimates adjusted for sleep may be appropriate.

Data structure of maternal socioecology

Next we explored the structure of Aka mothers' camp situation (Table 5). Note that all 17 variables in the analysis are counts of people around mothers in Aka camps. These variables indicate the sex and age structure of Aka camps, and include counts of alloparents, and presence of fathers and grandmothers. We wish to explore dimensions

TABLE 6. Principal components analysis for Aka mothers' camp situation

Variable	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6
Eigenvalues	3.55	2.70	2.07	1.85	1.77	1.55
Cumulative variance	0.21	0.37	0.49	0.60	0.70	0.79
Log adult males	0.28	0.18	-0.28	-0.09	0.09	-0.06
Log adult females	0.25	0.21	<b>-0.31</b>	0.04	0.01	-0.05
Log adolescent males	0.27	-0.10	0.15	0.17	<b>-0.47</b>	0.03
Log adolescent females	0.05	0.25	-0.16	0.12	<b>0.37</b>	-0.15
Log juvenile males	<b>0.54</b>	-0.08	0.11	-0.18	0.03	0.08
Log juvenile females	<b>0.48</b>	-0.02	0.04	0.14	-0.06	-0.05
Log brothers < 5 years	0.06	<b>-0.50</b>	-0.22	0.10	0.22	0.05
Log brothers 5-10 years	0.16	-0.13	0.07	<b>-0.66</b>	0.06	0.02
Log brothers 11-18 years	-0.01	-0.07	-0.13	0.08	-0.02	<b>0.73</b>
Log sisters < 5 years	0.04	0.12	<b>0.72</b>	0.02	0.02	-0.05
Log sisters 5-10 years	0.05	-0.06	0.08	0.02	0.62	0.11
Log sisters 11-18 years	0.04	0.15	0.14	-0.10	0.07	<b>0.61</b>
Log alloparents high I	-0.05	<b>0.51</b>	0.18	0.02	0.03	0.07
Log alloparents high II	-0.07	<b>0.44</b>	-0.07	0.12	0.13	0.03
Log camp size	<b>0.44</b>	0.11	-0.13	0.02	0.00	-0.02
Log grandmother	0.14	-0.14	0.12	<b>0.64</b>	0.06	0.06
Log father	0.09	-0.20	0.29	0.03	<b>0.40</b>	-0.14

Note: Component loadings greater than |0.3| are indicated in bold, defining the components.

of Aka camps using PCA; however, count data may give inaccurate PCA results especially when there are low mean values. We attempted to normalize these variables by a ln(X+1) transformation, then submitted the transformed variables to PCA.

PCA using Varimax rotation yielded six components with Eigenvalues >1 (Table 6). Component 1 is characterized by positive loadings for juvenile males (0.54), juvenile females (0.48), and camp size (0.44). Component 2 is characterized by both alloparent variables (0.51 and 0.44) followed by negative loading for brothers <5 years (-0.50). Component 3 is largely characterized by sisters <5 years (0.72), followed by a negative loading for adult females (-0.31). Component 4 is primarily characterized by grandmother (0.64), and by a negative loading for brothers 5-10 years (-0.66). Component 5 is characterized by father (0.40) followed by adolescent females (0.37) and a negative loading for adolescent males (-0.47). Component 6 is primarily characterized by brothers 11-18 years (0.73) and sisters 11-18 (0.61).

Effects of camp socioecology on maternal EE

We explored effects of camp socioecology using OLS regression and partial correlation analyses with bootstrapped P-values. Initially we used a backward elimination procedure to identify the strongest signals in the data. Predictor variables with bias-corrected accelerated bootstrapped (1,000 replications) P-values <0.05 were retained in each step in models (Table 7). EE comp 5 (sleeping) was included as a control variable. Comparing the first (full) and final (reduced) models indicates that Camp components 1, 2, and 4 are significant predictors of

TABLE 7. Multiple linear regression models showing effects of camp composition on Aka mothers' working EE (with bootstrapped *P*-values)

Variable	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>
EE Comp 5	-78.80	0.028	-77.94	0.018	-72.80	0.004	-68.20	0.004
Camp Comp 1	56.95	0.033	54.47	0.040	52.99	0.014	52.83	0.019
Camp Comp 2	-60.56	0.019	-59.58	0.015	-63.23	0.003	-67.10	0.002
Camp Comp 3	14.12	0.720	12.50	0.741				
Camp Comp 4	-53.06	0.044	-52.06	0.035	-50.90	0.019	-49.08	0.018
Camp Comp 5	-31.93	0.129	-31.79	0.106	-33.47	0.095		
Camp Comp 6	-11.51	0.745						
_cons	447.14	0.000	447.14	0.000	447.14	0.000	447.14	0.000
<i>R</i> -square, adj. <i>R</i> -square	0.55	0.39	0.54	0.41	0.54	0.43	0.49	0.40

*B*, unstandardized beta, bootstrap *P* is *P*-value obtain through bias-corrected accelerated bootstrap procedure with 1,000 replications. *R*-squared is the coefficient for the determination of the entire model, the first value is not adjusted, and the second value is adjusted. *P*-values < 0.000 indicate values less than 0.0005. Camp Comp 1 is defined by juvenile males, juvenile females, and camp size; Camp Comp 2 is defined by positive loadings for non-maternal caregivers and negative loading for brothers < 5 years; Camp Comp 3 is defined by a positive loading for sisters < 5 years and negative loading for adult females; Camp Comp 4 is defined by positive loading for grandmother and negative loading for brothers 5–11 years; Camp Comp 5 is defined by positive loadings for father presence and adolescent females and negative loading for adolescent males; Camp Comp 6 is defined by positive loadings for brothers and sisters 11–18 years.

TABLE 8. Multiple regression models showing effects of alloparents, grandmothers, and fathers on Aka mothers' working EE

Variables	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>
EE Comp 5	-62.6	0.105					-65.7	0.080			-61.6	0.085
Total juveniles	25.4	0.004	20.5	0.016	14.9	0.044	22.8	0.002	17.5	0.034	17.1	0.015
Nonmaternal caregivers	-10.7	0.024	-8.2	0.090			-11.8	0.017	-9.2	0.059	-10.8	0.028
Grandmother	-150.4	0.013	-138.7	0.017	-127.1	0.046	-128.6	0.036	-114.9	0.068		
Father	129.8	0.045	137.3	0.052	149.6	0.024						
Constant	409.9	0.001	401.0	0.001	279.8	0.006	521.8	0.000	519.3	0.000	475.5	0.000
<i>R</i> -square	0.44	0.32	0.31	0.19	0.23	0.13	0.33	0.22	0.19	0.09	0.25	0.15

We used multiple models to demonstrate the stability of the associations because of the small sample size. *B*, unstandardized beta; bootstrap *P* is *P*-value obtained through bias-corrected accelerated bootstrap procedure with 1,000 replications. *R*-square is the coefficient for the determination of the entire model, the first value is not adjusted, and the second value is adjusted. *P*-value = 0.000 indicates less than 0.0005. EE Comp 5 is sleeping EE. Number of siblings ( $P = 0.58$  and  $0.67$ ) and child age ( $P = 0.95$  and  $0.51$ ) were not significant predictors of work EE in the first or final model nor did they substantially influence the pattern of associations presented here.

EE, and sleep is a significant control. Component 1 (Table 6) is largely characterized by number of juveniles in the camp and camp size. Component 2 is largely characterized by nonmaternal caregivers. Component 4 is characterized by grandmothers. The final, reduced model accounts for between 49% and 40% of variance in maternal working EE. Nonmaternal caregivers reduce maternal EE by about 67 kilocalories per unit of Component 2. Grandmothers reduced maternal EE by 49 kilocalories per unit of Component 4. Presence of juveniles increases maternal EE by about 53 kilocalories per unit of Component 1. After obtaining the reduced model, we entered control variables for mother's age, child's age, and child's sex individually. None of the controls had *P*-values less than 0.8, and directions and magnitude of associations between Components 1, 2, 4 and working EE were largely unchanged and significant at the 0.05 level. Diagnostic analyses indicated that the final model did not deviate from the assumptions of multiple linear regression: there was no evidence of substantial leverage or multicollinearity, and a normal probability plot of model residuals indicated normal approximation.

In the penultimate step of the analysis, we entered alloparents, grandmothers, fathers, and juveniles into a model along with EE comp 5 (sleep). The first (full) model in Table 8 indicates that that nonmaternal caregivers, fathers, grandmothers, and total juveniles are significant predictors of Aka mothers' working EE. Sleep entered the models as a control variable with  $P < 0.10$ . The full model indicates that each nonmaternal caregiver reduced maternal working EE by 10.7 kcal, each juvenile in camp

increases maternal EE by 25 kilocalories per child, grandmothers decreased maternal EE by 150 kcal, and fathers increased maternal EE by 130 kilocalories. The final model indicates that each nonmaternal caregiver reduced maternal working EE by 10.8 kcal and each juvenile in camp increased maternal EE by 17.1 kilocalories per child. Following Table 5, the average Aka mother had about 12 juveniles in camp with her and 20 people who acted as a nonmaternal caregiver; given an estimated EE of 204 kcal for juveniles, and 216 kcal for nonmaternal caregivers, produces a total estimated EE of 761 kcal across the observation period. This should be taken as an estimate in addition to BMR rate of 422.48 across the observation period. Models 2 through 6 in Table 8 indicate model stability with selected variables removed.

Review of the added variable plots indicated one data point with very low working EE. Cook's *D* indicates no problem with leverage; however, we feel this point warrants further investigation. One woman had a very high score on EE Component 5 because she was observed sleeping almost twice as much as any other woman. We Winsorized this value by assigning EE component value of 2.08 (the next highest value) for the sleepy mother. Results of a multiple regression analysis using Winsorized values indicate no substantial change in the pattern or significance of results compared to the un-Winsorized analysis in Table 8; however, *P*-value for father increased to 0.08. Figure 1 below indicates the underlying residualized data in Model 1 of Table 3. Table 9 gives partial correlations for Model 1 in Table 8 with Winsorized EE comp 5 replacing EE Comp 5.

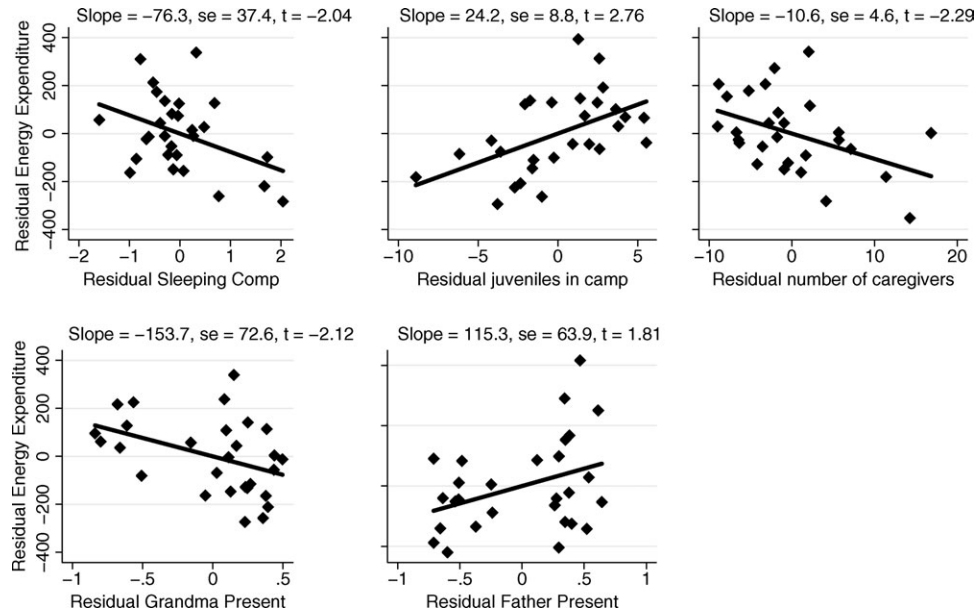


Fig. 1. Partial regression plots of maternal energy expenditure.

TABLE 9. Partial correlations with maternal-working EE

Variable	Partial Pearsons
Wins. Comp 5 (sleep)	-0.4124
Total number of juveniles	0.5145
Total number of caregivers	-0.4443
Grandmother	-0.4131
Father	0.3696

Note: Partial correlations for Model 1 in Table 8 with Winsorized EE Comp 5 replacing EE Comp 5.

Added variable plots show associations between predictors and criterion when other variables in the model are held constant. Figure 1 shows substantial effects of alloparents on maternal working EE. Grandmother and father are of particular interest and were coded as present (1) or absent (0). Plots indicating grandmother and father effects (Figure 1) show substantial variability for effects of classes of alloparent. Effects for fathers are especially interesting because recent theory suggests that husband effects on wives and children are especially variable cross-culturally (Hrdy, 2009). Variability is also apparent even among the Aka with “intimate” fathers. Additionally, differences in variance of maternal EE among “father-present” and “father-absent” mothers may suggest high heteroskedasticity. Stabilizing variance with a square-root transformation of the criterion variable (maternal EE) yielded *P*-values (not shown) slightly more conservative but approximately equivalent to those in Table 8; hence, heteroskedasticity appears not to be a problem in these models. Finally, the number of siblings ( $P = 0.58$  and  $0.67$ ) and child age ( $P = 0.95$  and  $0.51$ ) were neither significant predictors of work EE in the first or final model in Table 8 nor did they substantially influence the pattern of associations presented here.

TABLE 10. Descriptive statistics for direct childcare

Variable	Mean	SD	Min	Max
Frequency of mothers physical contact with child	598.39	233.67	89	1020
Frequency of fathers physical contact with child	28.79	77.21	0	401
Winsorized frequency of fathers physical contact with child	17.25	27.95	0	78
Frequency of grandmothers physical contact with child	36.39	77.83	0	333
Winsorized frequency of grandmothers physical contact with child	31.71	61.58	0	202

Note: Frequency of fathers and grandmothers physical contact showed one outlier each. Outliers were winsorized to the next lowest value.

#### Direct childcare and maternal EE

Thus, far regression models show that grandmothers reduce maternal EE, indicating a straightforward labor substitution, while fathers increase maternal EE. Next, we examine trade-offs in direct childcare (physical contact). Physical contact is comprised of two independent behaviors, “holding” and “touching.” Caregivers were coded as “holding” a child, if the child’s weight was supported in the caregiver’s arms, lap, or when the child was held in a sling attached to the caregiver’s body. “Touching,” either intentional or passive, was recorded when a portion of the child’s body was in contact with a caregiver. When holding and touching were combined, a caregiver’s frequency of physical contact with a child was obtained. Here we are interested in effects of grandmaternal and paternal direct care on mothers’ direct childcare. If paternal and grandmaternal care are substitutes for maternal care, then unstandardized coefficients for father’s and grandmother’s direct care should be negative and not significantly different from 1, indicating a one-for-one substitution of physical contact.

TABLE 11. Multiple regression showing effects of nonmaternal care on mothers' physical contact with child

Variable	<i>B</i>	Bootstrap <i>P</i>	<i>B</i>	Bootstrap <i>P</i>
Square root child's age	-48.58	0.020		
Total number of caregivers	-11.63	0.001	-14.14	0.000
Father's physical contact (winsorized)	-3.86	0.001	-4.66	0.000
Grandmother physical contact (winsorized)	-1.79	0.000	-1.59	0.000
Constant	1,134	0.000	1025.23	0.000
<i>R</i> -square	0.76	0.72	0.69	0.65

Note: Nonmaternal caregiving accounts for most of the variance in mother's physical contact with infants. Child's age is removed from the second model to demonstrate stability of associations. *B*, unstandardized beta; bootstrap *P* is *P*-value obtain through bias-corrected accelerated bootstrap procedure with 1,000 replications. *R*-square is the coefficient for the determination of the entire model, the first value is not adjusted, and the second value is adjusted. *P*-value = 0.000 indicates less than 0.0005.

Table 10 shows descriptive statistics for frequency of direct care. A zero-order correlation between maternal working EE and maternal direct care (frequency of physical contact) shows no association ( $r = 0.07$ ,  $P = 0.72$ ) indicating that trade-offs between work EE and childcare are not simple. We regressed the frequency of maternal physical contact on child's age, number of alloparents, frequency of fathers' physical contact with the child, and frequency of grandmothers' physical contact. Descriptive statistics and diagnostics for initial models (not shown) indicated potential outliers for both grandmaternal and paternal direct care. There was a single high outlier for both variables that we Winsorized to the next highest value (see Table 10). Additionally added variable plots (not shown) indicated substantial heteroskedasticity for child's age in months; hence, we took the square root of child's age to stabilize variance.

Table 11 shows effects of child's age and alloparenting on maternal direct care. Child's age, number of alloparents present in camp, father's physical contact and grandmother's physical contact were all negatively associated with maternal contact. Note that the model explains most of variance in maternal physical contact ( $R^2$  values are between 0.76 and 0.72). Each alloparent present decreases maternal contact by about 12 observations. Each bout of grandmaternal physical contact is associated with about 1.8 fewer bouts of physical contact with mother. Bootstrapped 95% confidence intervals for grandmaternal contact were between -0.96 and -2.61, suggesting a straightforward one-to-one substitution of grandmaternal care for maternal care. Each bout of paternal physical contact with the child was associated with 3.9 fewer bouts of maternal contact with bootstrapped 95% confidence intervals between -1.97 and -5.74, indicating that paternal direct care is not a simple substitute for maternal care. Taken together, these results suggest that fathers decrease the total amount of physical contact a child receives. Regression diagnostics indicated adequate models with minimal variance inflation, no outliers, and approximately normally distributed residuals. Other control variables (in Table 8) were not significant predictors of maternal physical contact.

We substituted paternal and grandmaternal physical contact for father and grandmother presence in the full model in Table 8 to test for effects of direct alloparental care on maternal working EE. Neither grandmother or father physical contact were significant predictors of

maternal working EE (not shown) and *P*-values were greater than 0.50. Taken together, results for working EE and direct care do not show a straightforward pattern of work/childcare trade-offs nor simple childcare substitutions. We discuss this pattern further in the conclusion.

## CONCLUSION

Multiple linear regression models indicate that nonmaternal caregivers have variable effects on Aka mothers' working EE. Grandmothers substantially reduce mothers' EE, whereas fathers and juveniles increase maternal EE. Partial regression plots indicate that both grandmother and father associations with maternal EE are quite variable. Grandmaternal direct childcare reduces maternal care by about one-to-one, indicating a straightforward labor substitution for both EE and childcare. Paternal direct care, however, tends to decrease maternal care more substantially, suggesting important differences in grandmaternal and paternal roles. How do we account for these differences?

That nonmaternal caregivers reduce maternal EE is not unexpected, particularly considering recent discussions of the evolution of human prosociality (Hill et al., 2011). However, magnitude of the reduction is notable—a 216 kcal reduction is approximately 28% of the 9-h EE estimate. Hill and colleagues argue that our understanding of hunter-gatherer cooperation has been hampered by a limited understanding of human prosocial behavior—hunter-gatherers are hypersocial, intensely cooperative, highly altruistic, and most importantly, cooperation extends beyond genetic relatedness—humans cooperate with kin and non-kin. Hunter-gatherers share food widely, display remarkable levels of allomaternal care, cooperate, particularly in food procurement, and share public goods daily (Hill et al., 2011). Although our study did not investigate resource contributions by others to mothers and children, our results indicate high levels of cooperation. The number of Aka nonmaternal caregivers reduces maternal EE—mothers expend less energy across the day when they have access to multiple helpers. The emphasis on network size, rather than individuals, also supports Ivey's (2000) research among the Efe, which suggested a significant positive association between the number of alloparents and child survival. However, examining the effect of nonmaternal caregivers as a whole does not capture the complexity of influences on maternal EE. When the effects of particular individuals or specific categories of caregivers are explored, results indicate that there are substantial differences in how particular caregivers influence maternal behavior.

The role of grandmothers and their impact on their daughters' reproduction has been extensively investigated over the last several decades (see Hawkes et al., 1997; Sear et al., 2000; Voland et al., 2005) although Hill and Hurtado (2009) recently suggested that the notable role of grandmothers may be overestimated, particularly in regards to provisioning in some forager populations (see also Hames and Draper, 2004). Ache and Hiwi grandmothers do minimal provisioning—female contributions to Ache subsistence are significantly lower than male contributions (Hill and Hurtado, 2009). Aka women, in contrast, contribute substantially to the diet, and even more so while living near villages (Hewlett, 1991). Consequently, we would predict that Ache grandmaternal provisioning is

limited by constraints on female food acquisition or the high degree of male provisioning, making their contributions less necessary. Hill and Hurtado (2009) leave open the possibility that grandmothers may be contributing through other means. Nevertheless, the cross-cultural variability in investment patterns by grandmothers across different subsistence strategies, cultures, and environments emphasizes that attention to the flexible nature of cooperative breeding (a key feature among humans) needs further attention.

That Aka grandmothers' presence reduces maternal EE suggests that these women are provisioning mothers and children. Postreproductive women are often observed carrying baskets that appear, at times, heavier than what was seen during our observations of mothers. In addition, many Aka grandmothers are widowed—grandmothers have little household responsibility beyond their own needs and may freely donate childcare and excess resources to their children and grandchildren. However, what is perhaps most interesting is that Aka grandmothers also offer a substantial amount of nonmaternal care, which would lead one to assume that grandmaternal childcare may also enable mothers' freedom to engage in nonchildcare activities. Results indicate that grandmaternal direct care acts as a substitute for maternal care. The dual role that grandmothers serve may be reflected in cross-cultural evidence indicating that women (and their mothers) position, or at least desire to position, themselves close to each other and benefit from this relationship (Gibson and Mace, 2005; Meehan, 2005; Scelza and Bliege Bird, 2008). Unfortunately, having a grandmother is far from guaranteed (Hill and Hurtado, 2009; Ivey, 2000). Previous research among the Aka showed that approximately 50% of children did not have access to a grandmother (Meehan, 2005). Here, the percentage of mothers with access to a grandmother is much greater because the sample is biased toward young mothers, which increases the likelihood that a grandmother is still living (Hill and Hurtado, 2009). Regardless, we did not find that grandmaternal direct care was associated with an increase in maternal EE. We argue that women with mothers or mother-in-laws in camp may be able to capitalize on the dual role that grandmothers serve. Women with provisioning grandmothers may not need to increase their EE toward work activities and grandmaternal investment in the form of childcare may simply allow mothers to divert more energy toward maintenance during the lactational stage. Future investigations focused on whether women with access to their mother and/or mother-in-law are able to achieve energy balance are clearly needed to fully investigate this conclusion.

In contrast to grandmothers, the presence of fathers increases maternal EE and decreases maternal direct care by greater than one-to-one: the unstandardized regression coefficient for paternal direct care (Table 10) is  $-3.9$  and 95% confidence intervals indicate the coefficient is significantly less than  $-1$ . Were fathers to offer a one-to-one childcare substitution with mothers, we might conclude, as set up in the introduction, that fathers enable mothers to shift strategies—fathers allow mothers to take advantage their high-quality care and increase energy toward labor activities. However, fathers do not offer a one-to-one childcare substitution; the frequency of paternal direct care is associated with a decrease in the amount of physical contact children receive. There are at least two possi-

bilities to explain this result: fathers might have longer bouts of direct care than mothers such that each bout of paternal care is 2.9 times longer than a bout of maternal care. If so, then paternal care may still be a rough substitute for maternal care; however, this is unlikely—the 30-s interval observation period should capture the longer bouts and Aka mothers have been previously shown to hold for longer durations (Hewlett, 1991). Alternatively, fathers may have different styles of childcare than mothers where childcare includes less physical contact and perhaps more distal interaction. Although, again, Hewlett (1991) suggests this is not the case among the Aka. Our results suggest that if fathers have a net benefit for offspring fitness, we must look elsewhere for the evidence. Perhaps, fathers improve Aka child growth, survival, or other components of fitness.

Studies on Aka fathers indicate that many, but not all, men spend substantial time in direct childcare (Hewlett, 1991, 1992; Meehan, 2005). Fathers spend more time in camp when residing near the village, but paternal holding does not differ between forest and village settings (Hewlett, 1991). This leads us to question why their presence decreases the frequency of physical contact. Paternal investment, particularly in camp settings, has been associated with mothers pursuing tasks unencumbered (Hewlett, 1991, 1992). However, lack of correlation between paternal direct care and maternal EE suggests that this is not the case. The presence of fathers increase women's energy devoted to labor and decrease the time mothers are in physical contact with their children. However, paternal presence shows no evidence of buffering childcare. The effects of Aka fathers on maternal EE are clearly different from what is found among the Ache and Hiwi where fathers reduce maternal foraging time (Hurtado et al., 1992). However, this is not unexpected. Ache and Hiwi men are responsible for the majority of calories and, as such, women are able to reduce the amount of time spent in subsistence activities when they have a high-producing husband. However, Aka women are responsible for a significant portion of daily calories, particularly when residing near the village (Hewlett, 1991). Greater EE for women with a husband present may indicate increases in production that are ultimately invested in offspring. Other interpretations, however, are possible and further research focused on subsistence returns, energy intake, and child outcomes is warranted.

The number of juveniles is also associated with an increase in maternal EE. Yet, despite their frequent child minding, their time allocation toward childcare is not associated with maternal EE. Ethnographic observations indicate that juvenile caregivers do not commonly offer care in the absence of mothers. They frequently offer temporary childcare when they travel with mothers during the day, but more often they are child minders in camp when mothers are engaged in domestic activities. That the number of juveniles increases maternal EE, but their direct care does not, suggests that juvenile contributions in childcare do not offset the increased energy that mothers devote toward labor in their presence. Age distribution in Aka camps is heavily biased toward juveniles (Hewlett, 1991). The high proportion of juveniles in Aka camps, combined with daily food sharing, may result in increased female EE regardless of reproductive status. In contrast, Maya children's economic contributions supplement maternal activity budgets and help to support their

younger siblings (Kramer, 2005). Without Aka juvenile activity budgets, which are not currently available, it is difficult to fully tease apart these results, but our results indicate that while Aka juveniles are frequent child minders, they may be a drain on Aka maternal EE.

It is important to note that nonmaternal caregivers may adjust their investment not only in regards to the mother's situation but also to the presence and investment by other caregivers (Kramer, 2010). For example, Aka nonmaternal investment is variable due to a multiple of demographic and social factors. Divorce, which naturally inhibits paternal care in infants and young children, is common. In addition, similar to compelling results among agricultural peoples (Leonetti et al., 2007), Aka fathers show highly variable investment based on postmarital residence patterns (Meehan, 2005). Aka fathers provide minimal childcare when they reside with their wife's family, but nonparental assistance from other adults and juveniles is ubiquitous. Alternatively, when a couple resides with her husband's family, nonparental care is minimal, but paternal investment is high (Meehan, 2005). Hrdy (2008) has suggested that a key feature of human paternal investment is its variability—male investment varies more among humans than all other primates combined. Given the flexible nature of nonmaternal investment, caregivers may adjust their investment level based on the level of support by others. Future research should address not only how others affect maternal strategies but also how individuals within the larger social or caregiving network affect each others' participation.

Our results demonstrate the utility of biocultural approaches to energetic studies. EE strategies are affected by the physical environment, subsistence patterns, and by a multitude of social and cultural factors (see: Piperata, 2008, 2009; Snodgrass, 2012). The integration of energetics with human behavioral ecology will enable us to explore how cultural strategies (subsistence economy, division of labor, settlement patterns, and social networks) affect health, fertility, and mortality in the face of changing lifestyles and ecologies (Dufour and Piperata, 2008; Leonard, 2004; Panter-Brick, 2002; Snodgrass, 2012). For instance, during lactation, heavy workloads, nutrition, and energy balance affect female fecundity (Jasienska and Ellison, 1998; Valeggia and Ellison, 2001). While time allocation and/or daily activity recall studies offer a contextual background to subjects' daily activities, data may overestimate or underestimate energy allocation toward specific tasks (Madimenos et al. 2011; Westerterp, 2009). Time allocation in broadly defined work activities may not necessarily involve high EE and Dufour and Piperata (2008) caution researchers to avoid making EE assumptions broadly based on subsistence strategies. Women spending equal time in labor activities may pursue vastly different energy allocation strategies, which will affect their energy balance, long-term health status, fecundity, and reproductive timing. Thus, a biocultural energetic perspective provides vital insights to life history studies (Snodgrass, 2012). Furthermore, with hunter-gatherer populations declining and facing increasing pressure, insights into hunter-gatherer EE are particularly critical at this time.

In sum, we have shown that maternal socioecology affects maternal EE—specific caregivers or categories of caregivers result in mothers decreasing or increasing EE and decreasing direct childcare. These results indicate that

there are multiple pathways by which helpers affect maternal behavioral strategies. Human offspring altriciality and extended dependency, as well as female life history traits would not be possible without the assistance of others (Hill and Hurtado, 2009; Hill et al., 2011; Hrdy, 2009). However, the extent of nonmaternal caregivers and their precise role has not been fully articulated. We contribute to this growing investigation by highlighting the breadth and diversity of influences on maternal EE strategies. We conclude that further research must explore the entirety of females' socioecology to understand how helpers affect female time allocation, EE, and maternal reproductive/somatic trade-offs.

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