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Infant allocare in traditional societies

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ABSTRACT

Across human societies infants receive care from both their mothers and others. Reproductive cooperation raises two important questions: how does allocare benefit mothers and infants, and why do caretakers help mothers when they could spend their time in other, perhaps more valuable ways? We use behavioral and biological data from three small-scale societies to evaluate 1) how allocare affects a nursing mother's time, 2) whether a mother's birth interval length, surviving fertility and infant weight vary as a function of the childcare help that she receives, and 3) the opportunity cost for helpers to spend time caring for children. Across our hunter-gatherer and agricultural samples we find that on average mothers provide 57% of the direct care that an infant receives and allocaretakers 43% (± 20%). Model results show that for every 10% increase in allocare the probability that a mother engages in direct care diminishes by 25%, a potential savings of an estimated 165 kcals per day. While allocare has a significant immediate impact on mother's time, no detectable effect on delayed fitness measures (birth interval and surviving fertility) or on infant weight status was evident. Cross culturally we find that other than mothers, siblings spend the most time caretaking infants, and they do so without compromising the time that they might otherwise spend in play, economic activities or education. The low opportunity cost for children to help offers an alternative explanation why juveniles are common caretakers in many societies, even in the absence of delayed indirect fitness benefits. While we expect specific patterns to vary cross culturally, these results point to the importance of infant allocare and its immediate time benefits for mothers to maintain flexibility in balancing the competing demands to support both older and younger children.

1. Introduction

Maternal investment is crucial to infant survival and wellbeing in all but the most wealthy, industrialized societies. Yet infancy presents an allocation problem for mothers who have young as well as older children to care for at the same time. Unlike other primates who usually terminate maternal provisioning at weaning, human mothers often have multiple dependents and face a tradeoff about whether to invest their time and energy in infant care or in activities, such as food production or wage labor, that benefit their older children [1]. Human mothers also are unusual in that others help them raise their offspring. Allocare, and more generally cooperative breeding, is a reproductive and social strategy in which group members other than parents assist mothers or their young [2]. Although relatively rare as a species-typical pattern in mammals, cooperative breeding occurs across diverse taxa, including primates, primarily small New World monkeys [3–6]. However because cooperative breeding is not a behavior shared by other great apes [7,8], it raises questions about why it emerged in humans and its relevant benefits and costs [9–13]. Here we specifically focus on allocare directed at infants (rather than juvenile care) to address how mothers benefit from help and at what cost to helpers who could spend their time and energy in other ways.

Interest in infant allocare in traditional societies has a rich history of study in anthropology, psychology and demography. While methodological approaches to mothers, infants and helpers vary across disciplines and researchers, several general observations can be made about infant care. First, in traditional societies the amount of assistance that mothers receive is variable, but often considerable. For example at 18 weeks, allo-caretakers provide 60% of the care that an Efe (Ituri forest hunter-gatherers) infant receives [11]. When observed in camp, Aka (central African hunter-gatherers) mothers held their young infants (1–4 months old) 51% of daylight hours, fathers 22% and others 28% [14:pg 269]. For the Hadza (east African hunter-gatherers), the time that infants interact with someone other than their mother doubles between the first and second year, increasing from 22% to 56% [15]. When aggregated over the first four years of life, Hadza children are held 31% of the time by allomothers [16]. Among the Savanna Pumé (native South American hunter-gatherers), 49% of the direct care

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received by a breastfeeding infant is provided by someone other than the mother. In contrast to other groups of hunter-gatherers, Howell [17] notes that !Kung (Kalahari hunter-gatherers) mothers account for 75–80% of all physical contact that an infant receives in the first 20 months of life [18]. These case studies make the point that allocare is both prevalent and variable in human societies.

The second general observation is that allocare appears to be an effective strategy to offset maternal constraints in supporting both younger and older children. For example, among Aka hunter-gatherers and Ngandu agriculturalists of central Africa, although mothers hold their infants less when they are engaged in work, allomothers compensate for this decrease in maternal care [19,20]. Among the Kipsigis, African pastoralists, the quality of care that allo-caretakers and mothers provide was found to be comparable as measured by infant distress [21]. Rural Brazilian women who have social support, which includes childcare, food provisioning, subsistence and domestic help, lost less weight during lactation than women without social support [22]. In managing the competing demands of younger and older children several studies show that mothers, depending on their subsistence base, spend less time foraging for food, in agricultural work, domestic activities, or wage employment when they have a nursing infant. Instead, mothers give priority interest to childcare [1,15,23–25]. For example, among Maya subsistence farmers, mothers with young nursing infants spend no time working in the fields, a food production investment that benefits older children and requires mothers to travel several kilometers from home [25]. In these cases fathers, siblings and others compensate for the reduction in maternal economic activity. Other studies find that mothers with young children do not spend less time foraging or in other productive work [20,26], rather they receive more help caring for young children [19].

To consider who helps infants cross culturally, we assemble published data from nine traditional societies (Fig. 1). To be both comparable to each other and consistent with the behavioral-observation data used in our analyses, the studies included use similar time allocation methods and report on who provides the direct care that an infant receives (e.g. infants receive a certain amount of care, mothers provide some portion of that care, and others provide the balance). In most of these ethnographic cases direct care includes physical contact such as breastfeeding, holding, carrying, feeding and grooming [11]. While mothers devote the most time to infant care, allo-caretakers provide nearly half of the care infants receive. This regularity is striking and in part may reflect that maternal breastfeeding constitutes a large proportion of the direct care that a child receives. For example, among the study populations analyzed here, breastfeeding comprises on average 38% of a mother's direct care. Since infant survival in traditional societies is dependent on mother's milk [27], there is likely a limit to the minimum amount of time mothers spend in direct care regardless of the availability of helpers.

Because much of infant care is provided by someone other than a mother, allocare has important implications for understanding both female life history and the costs and benefits of reproductive cooperation. We use three behavioral and biological datasets, two from a group of subsistence farmers and the other from a group of hunter-gatherers, to address 1) whether the help a mother receives affects the time she allocates to direct care, breastfeeding or economic activity, 2) how the help mothers receive affects long-term fitness outcomes (birth intervals, surviving fertility) and child weight status, and 3) whether those who spend the most time caring for infants compromise the time that they might spend in other activities, such as education, economic work or play. Before turning to the analyses, we discuss human life history and how infant care differs from other kinds of helping behaviors.

1.1. Infant care and how it differs from other helping behaviors

Since most mammalian cooperative breeders raise offspring to independence during infancy, helpers assist breeding females and their

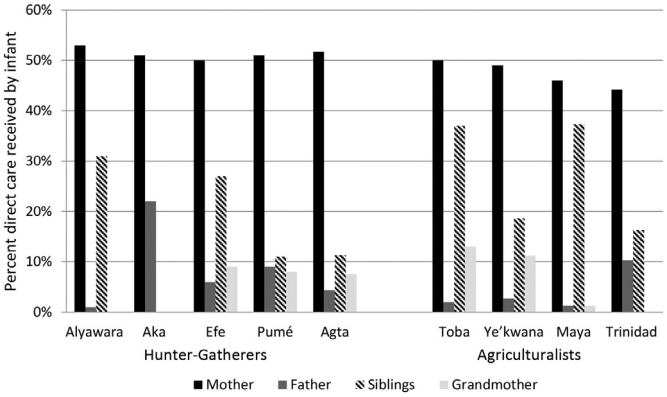


Fig. 1. Percent of direct care received by an infant that is provided by mothers and allo-caretakers. Missing values indicate no reported data. Unless otherwise specified below, direct care includes nursing, feeding, carrying, holding, grooming (dressing, bathing, delousing, minor medical) and playing with an infant. Any comparative assessment between studies should consider differences in methods. Within group values sum close to 100% in all cases except for the Agta for unreported reasons.
Sources: **Alyawara** [114:pg 264]; observation period unspecified; infant focal follow data; n = 495 observations, n = 18 infants (ages unspecified); values reported for carrying an infant only. **Aka** [14:pg 269]; observation period 6:00 am–6:00 pm; infant focal follows; n = 6 children ages 1–4 months; values reported for the mean percent of time mother, father and others held focal infants during daylight hours (because infants are held 100% of daylight hours, this is equivalent to the proportion of care receive by an infant); observations are for babies while they are in camp only; values reported for holding only (because holding includes playing with, carrying, cleaning, nursing and feeding it is largely inclusive of what other studies refer to as direct care); in addition to fathers, 'others' are reported to hold focal infants 27.8% of daylight hours, but who 'others' refers to is unspecified. **Efe** [Ivey unpublished data]; observation period 12 daylight hours; focal follow data; n = 20 children (ages unspecified). **Pumé** [Kramer and Greaves unpublished data]; observation period 6:00 am–6:00 pm; instananeous scan sampling data; n = 892 observations, n = 11 breastfeeding children ages birth to 3. **Agta** [115:pg 1206]; observation period 5 am–7 pm; scan sampling data recorded at 8 standardized time points across the day; n = 282 child days for children under age 11; specific activities included as childcare unspecified. **Toba** [93:pg 106]; observation period dawn to dusk; instananeous scan sampling data; n~24 infants < 24 months. **Ye'kwana** [23:pg 245]; observation period 7:00 am–7:59 pm; instaneneous scan sampling data; n = 16 children ages 0–40 months. **Maya** [116:pg 227]; observation period 7 am–6 pm; instaneous scan sampling data; n = 314 observations, n = 9 breast feeding children ages birth to 3. **Trinidad** [117:pg 66]; observation period unspecified, instantaneous scan sampling data; children ages 0–4, n unspecified; grandmothers are not reported separately, but included as 'other'.

milk-dependent young [2]. In humans, children are weaned at a young age and juveniles are at least partially subsidized with food, shelter and other resources. The redistribution of offspring dependence across these two life stages is significant to questions about cooperative breeding because helping an infant versus a juvenile has very different implications [28] (Fig. 2). First, caring for an infant entails carrying, holding, feeding, babysitting and the like, which are activities that helpers do not otherwise do for themselves. Second, assistance flows in one direction, from helpers to infants; others help infants, but infants are too young to reciprocate. In contrast, juveniles consume adult foods and resources and provisioning a juvenile is embedded in the same suite of tasks that helpers otherwise do to support themselves. Further, in most preindustrial societies, juveniles are important food producers, share food with others, contribute to household labor and take care of their younger siblings [29–34]. For example, Hadza children living in sub-Saharan Africa spend 5–6 h a day foraging for food. By the age of 5, they supply about 50% of their own calories during some seasons [35:pg 367]. !Kung children spend little time foraging [17], but by the age of eight crack most of the mongongo nuts they eat, which constitutes a substantial portion of their diet [36]. Specific to the groups that are the subject of this analysis, Maya children produce 50% of what they consume by age six [37], and much of what they produce is shared with other household members. Among the Savanna Pumé, South American hunter-gatherers, juveniles make important contributions to



Fig. 2. Savanna Pumé mother balancing childcare with cooking food for her older children. Photo credit Russell D. Greaves.

other camp member's energy budgets on days that they forage [38]. For example, boys have an average return rate (amount of food produced per foraging trip) of 4.5 K of wild fruit (~3200 kcal). This is what they return to camp after whatever field snacking they might do and is a sufficient calorie return to feed himself and at least some of his family.

In sum, infant care is a potentially costly expression of cooperation because it involves tasks that helpers otherwise would not do to support themselves and infants are obviously too young to reciprocate. Given this, two general explanations have been suggested to explain why helpers help infants and young children.

One hypothesis proposes that helpers directly benefit by learning skills that enhance their future success in raising offspring of their own [11,39–45]. For example, among vervet monkeys longitudinal data show that females who spent more time carrying infants as juveniles, were significantly more likely to have a first born who survived [46]. One prediction this parenting experience hypothesis generates is that human children who help the most will grow up to have better reproductive outcomes. In testing this prediction, we previously found inconclusive evidence; Maya girls who spent more time in allocare as children did not have more surviving offspring as adults [47]. That analysis used time allocation data were collected in 1992 over the course of a year [32], and the reproductive histories of these Maya girls followed for the next 20 years. Model results were suggestive in that girls who spent at least some time in allocare (5–15%) had higher fertility outcomes, but at a diminishing marginal return. Girls who spent > 20% of their time caring for their siblings (some girls spent as much as 30% of daylight hours in childcare) did not have higher fertility than those who spent < 20%. The challenge of testing this hypothesis is the rarity of longitudinal datasets with sufficiently large samples that track girls from childhood through their reproductive careers. Although the Maya results were statistically ambivalent and limited by sample size, this is a provocative question for future research.

Another hypothesis proposes that helpers benefit indirectly by augmenting the reproductive fitness of their close kin [48]. The theoretic expectation is that because helping incurs a cost, it should be offset by an indirect fitness benefit. Kin selection has had broad appeal as the evolutionary basis for cooperative breeding [49–54], and is empirically evidenced by the close genetic relatedness often noted across species between helpers and those they support and the amount of allocare they provide [55–57]. Likewise human infant allocare is typically, but not always, kin based [11,16,23,58].

While kin selection is a predominant explanation for why helpers help, recent research also emphasizes that the focus on indirect benefits may eclipse direct benefits and overstate the cost to help [2,52,59–62]. For example an individual may directly benefit if caring for another's offspring reduces parental workloads and augments group size [63–65]. Helpers may also directly benefit by engaging in mutualistic cooperative interactions [60]. To this we add that the opportunity cost to spend time caring for an infant is an important consideration because it is age-specific and dependent on reproductive status [28,33]. The cost to help is attenuated, for example, for both sexually immature juveniles and postreproductive females since they are not competing for mating opportunities or physically supporting reproduction. Young juveniles additionally have fewer other competing productive ways to spend their time since they are skill and strength limited [66,67].

1.2. Research questions

Thus to explain allocare and reproductive cooperation, the expectation is that the cost to provide care is compensated by some fitness benefit to mothers or infants (and in so an indirect benefit for helpers), and/or that the cost to help is not particularly high. Here we use data from three traditional populations to first evaluate the benefits of allocare to a mother's time and fitness. Specifically, what affect does allocare have on how mothers spend their time, and what are the effects of childcare help on interbirth intervals, surviving fertility and child weight status? Second, we consider the cost of allocare. In particular for those who help the most, what is their opportunity cost to spend time caring for children?

2. Materials and methods

2.1. The ethnographic samples

To evaluate these questions, we draw on behavioral and biological data that were collected in two traditional populations at three time points. The Savanna Pumé are mobile hunter-gatherers who live on the llanos of west-central Venezuela [32,68,69]. The time allocation, breastfeeding and anthropometric data used in the analyses were collected in 2006 and 2007. The Maya are subsistence maize farmers who live in a remote area of the Yucatan peninsula, Mexico [32]. Two time allocation, breastfeeding and growth samples were collected in the same Maya community, in 1992 and 20 years later in 2011. The sample of mothers and infants from the two time periods are independent and do not overlap. Our description of the Savanna Pumé and Maya focuses on those factors that affect mother, infant and allo-caretaker interactions.

Because of Venezuela's political instability and economic collapse, and the Savanna Pumé's geographic isolation, they are buffered from outside encroachment and have maintained a hunting and gathering way of life [69]. Women marry at a young age (mean = 15.1 ± 2.5, n = 59), and 90% have their first-born child between ages 15–19 [70]. Due to high rates of spousal death and divorce, nearly 40% of adults remarry [71]. While marriages tend to be serially monogamous, 20% of women and 11% of men marry polygynously at some point in their lives. Although average completed fertility for women over the age of 40 is 7.0 (± 1.29; n = 18), child mortality is high. Young children are particularly challenged to survive their first wet seasons during which food availability and the quality of mother's milk declines and disease exposure is high. Of children born, 35% do not survive infancy [72].

In contrast to the Savanna Pumé, the Yucatec Maya have undergone substantial change over the last 20 years due to the introduction of a paved road and subsequent access to mechanized farming and the regional economy. While their subsistence economy has changed, many aspects of their reproductive lives remain the same. During both time periods (1992 and 2011), Maya marriages can be described as life-long and monogamous; divorce has never been documented in the reproductive histories collected annually since 1992 (n = 214 married adults) and male reproductive skew is very low [73]. Some women (~25% in the 2011 sample) currently use birth control, although mean completed fertility has only marginally declined over the past 20 years

(1992 mean = 7.5, ± 1.74, n = 24; 2011 mean = 6.1, ± 3.01, n = 40). Infant mortality is relatively low for a traditional population, which can be attributed to the region's sparse population density and the use of closed-wells as the source of water (there are no rivers in this part of the Yucatan peninsula) [74]. Infant survival is estimated to be 96% (IMR = 37/1000), and has not significantly changed between the two time periods [75].

Although the Savanna Pumé and Yucatec Maya have very different subsistence economies, mother-infant interactions are equivalent in many ways. In both societies and across time periods, prolonged and intensive breastfeeding are the norm [75–77]. Babies sleep with their mothers, and are breastfed on demand during both the day and at night. Supplemental foods are introduced at about six months, and weaning occurs between the ages of two to three, as is the norm in natural fertility populations [78]. By age three or four, children perform simple domestic tasks, run food, information and errands between households and take care of their younger siblings [32]. The Savanna Pumé live in camps of clustered open-walled structures which are in close proximity. Likewise, the Maya live in a small village and mothers have access to a range of caretakers. In both societies, childcare is relatively fluid and babies are readily passed among siblings, fathers, grandparents, and more distant relatives. For example, among the Savanna Pumé, an infant on average has nine caretakers beside their mother (range 5–12).

2.2. Data collection

The three time allocation samples (Savanna Pumé 2006–7, Maya 1992, Maya 2011) were collected by the authors using the same standard instantaneous scan sampling methods, coding scheme and protocols [32]. The methods were developed by KK for the 1992 Maya study, and used by KK and AV in the subsequent Maya and Savanna Pumé time allocation studies. Instantaneous scan sampling is a behavioral observation technique widely used in both animal and human studies to measure the frequency of activities [79–81]. Over repeated observations, instantaneous scan sampling is a reliable method to estimate the proportion of time that an individual spends in various activities [79,82,83], and is considerably more accurate than interview or survey data to estimate time budgets [84]. During a scan sample, individuals are located at specific time intervals, and the researcher instantaneously records what they were doing. Over 400 types of activities were coded, which in addition to childcare include subsistence work (foraging, fishing, hunting, fieldwork), domestic work (collecting firewood, water, processing food, cooking, sewing, washing and the like), children's play, social, leisure and hygiene activities. The same methods and suite of hierarchical codes were used to record mother, infant and caretaker behaviors (see Table S1, supplementary materials for an example of childcare codes). In cases where a caretaker's primary responsibility is caring for a child but they are also doing something (for example, when children mind older babies, they might also be playing), the behavior was designated as such and coded as indirect care (see Table S1 supplementary materials). Scan samples were collected during daylight hours (7 am-6 pm) and variables recorded included the individual's identification number, his or her activity, the object of the activity (in the case of childcare, the object is the id of the person either doing the caring or being cared for), the location, date and time (for detail on time allocation methods see [32]).

Across the three ethnographic samples, the database consists of nearly 50,000 scan observations (n = 49,801; Table 1). These observations are the basis to calculate 1) the probability that a mother allocates time to direct care, nursing or an economic activity, 2) the proportion of care that an infant receives from their mother versus an allo-caretaker, and 3) the proportion of time that children spend in allocare, play, education and productive work (calculated as the number of scan observations coded for the activity divided by the total number of observations for the individual).

The Savanna Pumé scan data were collected on all camp members (n = 72 individuals) across two field seasons in 2006 and 2007 and includes 10 nursing mothers and their infants. The Maya scan data were collected for a subset of the community (112 individuals or 30% of total population in 1992 and 91 individuals or 18% of total population in 2011), which includes 9 nursing mothers and their infants in 1992, and 8 mothers and their nursing infants in 2011.

Demographic and reproductive history data (maternal age, completed and surviving fertility and birth interval length) are taken from census databases maintained by KK since 1992 for the Maya, and since 1991 for the Savanna Pumé. For children born during a field season, birth dates are known to the day. For children born between field seasons, parents can accurately report the ages of infants in moon counts (months), and young children up to 3 years in season counts (6-month units). For the Maya, birth records were available for the children in the 2011 sample, and retrospectively for many children in the 1992 sample. Anthropometrics for both Savanna Pumé and Maya children were collected by KK using standard procedures and equipment for children [85].

Research protocols and consent procedures were approved by the University of New Mexico's Institutional Review Board (Maya 1992 data), Stony Brook University's Institutional Review Board (Savanna Pumé data), and Harvard University's Institutional Review Board (Maya 2011 and Savanna Pumé data).

2.3. Terminology

Consistent with other analyses of human childcare, we subset infant care into direct and indirect care. Direct care refers to intimate behaviors that imply close physical proximity, and includes nursing, feeding, carrying, holding and grooming (dressing, bathing, delousing, minor medical). Indirect care refers to behaviors such as walking with, laying in a hammock or playing with a child, talking to or giving a child a directive, comforting a child, watching or keeping a child out of trouble. Direct care and indirect care are mutually exclusive behavioral categories and are a composite of more detailed behavioral observations (see Table S1 supplemental materials). (Note that direct and indirect childcare are both forms of direct investment, sensu Kleiman and Malcolm 1981 [86], and indirect childcare is not to be confused with indirect investment [86], which refers to territory defense, nest construction, resource provisioning and the like). Throughout infant refers to a nursing child. Child, children, juvenile are used generally to refer to subadults. The terms helper, allomother and allo-caretaker are used interchangeably.

2.4. Statistical analyses

We conduct three sets of analyses. In the first we consider the effect that allocare has on a mother's time. Here we use the scan database to model the probability that a mother engages in direct care, breastfeeding or economic activity as a function of the amount of allocare her nursing infant receives. We use a generalized linear mixed model approach (proc glimmix; SAS version 9.4) with options specified to account for the binary distribution of the dependent variables (direct care 0,1; breastfeeding 0,1; economic activity 0,1), and for repeated observations on mothers. For this analysis we limit the scan data to mothers with nursing babies, and code each maternal observation as 1 if a mother was engaged in direct care, breastfeeding or economic activity, depending on the model, and 0 for all other activities (n = 5406 scan observations for 27 mother-nursing infant dyads). Child age (at the time of each observation) is added as a control variable. Mother's id is nested within group (Savanna Pumé, Maya 1992, Maya 2011), which is specified as a random effect to account for differences in intercepts and slopes between groups. This hierarchical modeling structure allows us to account for group differences in the distribution of allocare (see Table 1), and permits estimation with unequal numbers of observations per mother and differences in sample size. Allocare is specified as a

fixed effect and calculated as the sum of direct care observations that an infant receives from someone other than its mother divided by the sum of all direct care observations that the infant receives. Indirect care and combined direct and indirect care were also considered and calculated in the same way. For ease of interpreting the parameter estimates, these proportions are multiplied by 100 and expressed as a percent.

In the second set of analyses, we use OLS regression to consider the effect that allocare has on three fitness outcomes: birth interval length, surviving fertility and child weight status (dependent variables). These outcomes are modeled as a function of the help that a mother receives (main predictor, using the allocare variable described above, which is the proportion of care received by an infant given by an allo-caretaker). Maternal age (at the time of observation) and group (represented as dummy variables 1/0, 0/1, 0/0 for the Maya 1992, Maya 2011 and Savanna Pumé, respectively) are added as control variables. Here summary data (each individual is a row) are used for the 27 mother-infant dyads. The outcome birth interval is defined as the duration between the birth of the nursing child to the birth of the next child, and surviving fertility as the number of surviving children at the time of observation. Since children in the samples are not the same age, child weight status is expressed as weight converted into 2006 WHO z-scores using the LMS method [87,88] (the 2006 WHO data are for breastfed and ethnically diverse children ages 0–5).

In a third set of analyses we consider the opportunity cost of allocare. We focus on children ages 3–15 because across the three populations they are the age class of helpers who spend the most time in allocare (see Fig. 1). To determine whether the time these children spend caring for their siblings detracts from other ways they might spend their time, we use a general linear model structure controlling for a child's age and sex. The Maya 1992 sample includes 43 children, the Maya 2011 sample 33 children and the Savanna Pumé sample 27 children. In this analysis, the scan observations for childcare, work, play and education were summed by individual and expressed as the proportion of a child's total number of observations. If spending time caring for infants incurs a cost to helpers, we expect that the time spent in childcare will have a significant negative relationship with the time children spend in education, play or economic activities, while no relationship or a positive relationship would indicate an insignificant opportunity cost.

Statistical and descriptive analyses were conducted using SAS version 9.4, and SPSS Statistics 22 (IBM Corp., 2013). IBM Corp. (2013). IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.

2.5. Data limitations

Ages for infants and their mothers are known to the day for the Maya. However ages are less precise for the Savanna Pumé, who do not keep vital records nor have a numeric calendric system, and thus cannot retrospectively state their age. These limitations are common among hunter-gatherers and a number of field methods were employed to construct reliable age estimates [72,89,90]. Savanna Pumé parents and other camp members can reliably recall young children's ages in moon (month) and season (6-month) counts; birth dates are known to the month for 56% of children under the age of five, and all children under the age of two. For older children and adults, ages were ascertained from multiple methods such as annual censuses and reproductive history interviews, rank-ordered sibships and age-graded kin terminology [91,92]. Consequently in the Savanna Pumé sample, some birthdates are known to the day (if we were present during a birth), and others to the month, season or year. The variation in birthdate precision introduces uncertainty around some age estimates. The analyses using the summary data to determine the effects that allocare has on fitness outcomes should be considered exploratory since it relies on data organized as mother-infant dyads and the sample size is small (n = 27). Because the authors collected the time allocation data at different time points (KK the Maya 1992, AV Maya 2011 and AV the Savanna Pumé sample), some coding differences may exist between researchers. Although we cannot retrospectively assess inter-observer consistency, we suspect this to be minimal since the same hierarchical coding scheme was used for all three samples, we are observing behavior (rather than intention or emotional states, such as infant distress), KK trained AV in time allocation methods and was present in the field to address coding questions. Scan samples were collected only during daylight hours, a limitation in most time allocation studies in traditional societies. This likely minimally affects the observation of economic activities since the Maya and Savanna Pumé were also limited by the lack of light at night. However, it may introduce some bias in reported proportions of who provides childcare if providers (mothers vs allocaretakers) systematically shift during nighttime hours. While our analyses focuses on the proportion of time spent in childcare and thus scan sampling methods are appropriate, focal follows, which measure the duration of an activity, may give further insight into infant care, in particular into maternal breastfeeding patterns.

3. Results

3.1. Descriptive statistics

Of the direct care received by an infant, on average 43% (± 20%, n = 27 mother-infant dyads) was provided by an allo-caretaker (Table 1). Although differences in allocare among the three groups are not significant (f = 1.97; p = .16), we make several observations about our samples. The decrease in allocare between the Maya 1992 (52%) and Maya 2011 (43%) is modest (pairwise d = 0.43, ci = 0.27–0.58), but consistent with other studies that find an association between market integration and young children being cared for more often by their mothers [93]. Between 1992 and 2011 regular schooling was introduced, which limits the availability of juvenile caretakers. The lower average level of allocare among the Savanna Pumé (34%; d = 0.54; ci = 0.39–0.63) may reflect the high child mortality in this group and its effects on diminishing both the availability of helpers and demands on a mother's time [72].

Across the three samples, nursing mothers spend on average 11% of daylight hours (± 6%, range 3–29%, n = 27 mother-infant dyads, 5406 scan observations), or 1.2 h per day in direct care (average age of children is 1.73 ± 0.93, see Table 1). Of the time mothers allocate to direct care, 41% of observations are for breastfeeding. Averaged across the three groups, of observations for nursing babies, 6.4% are for breastfeeding (equivalent to 42 min/day) and 22.1% are for direct care (146 min/day). Mean surviving fertility was 4.2 children per mother and the average time to next birth was 2.8 years. Child weight averaged 8.9 k, and children were 54% of the mean five-year-old weight for their respective populations. The only variables that significantly differed between the three groups were surviving fertility and achieved percent of 5-year-old weight (see Table S2 supplementary materials for pairwise Cohen's d for the main predictor and outcome variables).

3.2. What effect does allocare have on a mother's time?

We use generalized linear mixed models to evaluate the probability that a mother with a nursing child will invest in direct care, breastfeeding or an economic activity as a function of the allocare that the infant receives. We find that mothers whose infants receive a higher proportion of allocare have a significantly lower probability of engaging in either direct care or nursing ($\beta = -0.025$, p = .013; $\beta = -0.016$, p = .025, respectively, n = 4878 scan observations, Table 2). This result can be interpreted as a 1% unit increase in the allocare that an infant receives affects a 2.5% decreases in the probability that a mother will engage in direct care and a 1.6% decreased probability she will engage in a breastfeeding observation. Indirect care, a more passive form of allocare, has no effect on a mother's probability of engaging in either direct care or breastfeeding (Table 2).

When direct and indirect allocare are combined it also has no effect on a mother's time (Table S3 supplemental materials). The level of allocare has no effect on the probability that a mother will engage in an economic activity ($\beta = 0.001$, $p = .950$; $\beta = 0.017$, $p = .166$ for direct care and indirect care, respectively; Table 2, Table S3 supplemental materials).

3.3. Do mothers with more help have better fitness outcomes?

For the dependent variable birth interval, the sample is limited because some mothers were either at the end of their reproductive careers or a subsequent child was not born during the observation period (16 mothers closed a birth interval). Allocare was not a significant predictor of birth interval length, controlling for maternal age and group ($\beta = -0.261$, $p = .836$; Table 3; Table S4 supplemental materials). Nor was allocare a significant predictor of surviving fertility ($\beta = 1.943$, $p = .084$), or child's weight status ($\beta = -1.346$, $p = .262$). Thus, the amount of allocare that a mother's infant receives, controlling for her age, appears to have a weak statistical effect on maternal birth intervals, surviving fertility, and child's weight status.

3.4. What is the opportunity cost to help?

In the final set of analyses we consider the cost to help for those who spend the most time helping. Across the three focal groups, siblings provide between 11 and 37% (Savanna Pumé and Maya 1992, respectively) of the direct care received by a nursing infant, more than fathers, grandmothers or other relatives. Children 7 to 14 years old allocate the most time to childcare (direct and indirect care; Fig. 3), and may spend upward of 16% of daylight hours caring for their younger siblings. This is comparable to the Hadza, among whom subadult helpers (ages 1.5–17.9) may spend up to 20% of their time holding other children [16].

To assess the opportunity cost of being a caretaker we ask whether children who spend a greater proportion of their daytime hours caring for their siblings (direct and indirect care) spend less time in activities that might otherwise benefit them. For the Maya 1992 and 2011 samples, after controlling for age and sex, childcare does not covary with a significant decrease in time spent in economic activities or education (Table 4; Table S5 supplemental materials). Maya 1992 children, however, who spent more time caring for their siblings spent significantly less time in play ($\beta = -0.662$, $p = .034$). Because the Savanna Pumé have no schools, we consider whether time spent in allocare negatively impacts foraging for food or playing. In this case allocare is not a significant predictor of time spent in these alternate activities.

4. Discussion

We draw three main conclusions from our analyses of allocare in traditional societies. First, all mothers receive some help caring for their infants, which has a significant effect on their time budget. Across individuals in our focal groups, of the direct care that an infant receives minimally 10% and upward of 77% is provided by an allo-caretaker (average 43%; see Table 1). Our first set of analyses (see Table 2) showed that mothers who received more help had a significantly lower probability of engaging in direct care. The parameter estimates tell us that for every unit increase in help, the benefit to a mother's time more than doubles (for every 10% increase in the help a mother receives, the probability that she will engage in direct care diminishes 25%). Given that the direct allocare received by an infant ranges from 10% to 77%, help can make a substantial difference to the time budgets of many mothers. Looked at another way, across our samples mothers spend on average 11% of their time in direct care (range 3–29%, ± 6%). Every 10% increase in infant allocare saves a mother on the order of 165 kcals per day, which can be reallocated in other ways. (10% of maternal time is equivalent to 66 min per day, which at a PAR level of 2.5 kcal/min for direct childcare, is a savings of 165 kcal. The calorie estimate will be higher or lower depending on PAR assumptions, see [94,95] for PAR estimates).

Although we anticipated that mothers who received more help with infant care would increase their breastfeeding frequency, the results indicate that they do not. This raises several points. Mothers are cognizant of breastfeeding benefits, and prolonged intensive breastfeeding is the norm in most traditional societies [96], as it is for the Maya and Savanna Pumé [77,97]. Thus regardless of the amount of help received, there is likely a limit to the minimum amount of time that a mother spends nursing. But why with more help, do mothers breastfeed less often? Nursing at times also functions as an opportunity to bond with an infant and to provide comfort rather than nutrients per se [98]. In these roles, helpers perhaps can readily substitute for mothers by carrying, holding and playing with infants. Exploratory analysis suggests that this might be the case. In our three samples, nursing frequency increases when mothers receive some help, but declines at high levels of allocare (Fig. S1 supplemental materials). Because this relationship is independent of the child's age, it suggests that some portion of time spent breastfeeding serves ends other than nutrition and helpers substitute for mothers by providing other forms of direct care. We also note that in both societies, infants are frequently laid in hammocks. Because hammocks protect young children from many dangers, they may substitute for direct care on occasion, and in part explain why, for example, Aka infants under the age of 4 months are continuously held [14], while Savanna Pumé and Maya infants are not.

Given that mothers in natural fertility societies are balancing the competing demands of supporting younger and older children, we might expect that if others help, mothers would reallocate the saved time to economic activities that benefit her older children. This however is not the case; the help that mothers receive did not covary with maternal economic activity. Across our samples, mothers with nursing children spend on average 13% of their time in leisure (socializing, in personal maintenance, resting and the like), which is less than an hour and a half per day. This is much less, for example, than Aka women who spend 64% of their time in leisure [19,20]. This suggests that the nursing women in our sample may already be at a maximum in the time they allocate to economic activities. From previous study we know that nursing Maya mothers with babies less than a year old spend 33% of their time in childcare, 13% more time than mothers with older babies [25]. They also spend 10%, or 1.1 fewer hours per day in domestic and subsistence activities. Thus, overall Maya mothers spend equivalent amounts of time to non-leisure activities, but nursing mothers appear to shift their effort from domestic and economic work to childcare when they have young infants.

Our second finding is that although allocare has an immediate time savings advantage for mothers (mothers who receive more help spend less time in direct care themselves), delayed fertility benefits were not statistically evident. Mothers who received more help did not have higher surviving fertility or shorter birth intervals, nor did they have better child weight outcomes (see Table 3). While we are working with a limited number of mother-infant dyads and more significant associations might emerge with a larger sample, the effects of allocare may be diluted when outcome measures are time delayed. For example, maternal fertility is a cumulative, long-term process during which the presence of allo-caregivers and their level of help likely fluctuate, and are affected by many other variables beside the availability of help. The long-term fertility benefits of infant allocare have been evaluated using demographic data, but have rarely been tested with observational data. Our behavioral data and results suggest that the benefit of allocare to mothers may be more immediate.

This has implications for why helpers help and who helps. The lack of evidence for positive indirect fitness benefits may in part be due to the time delay between when help is given and the outcome measured. However, we also suggest that when fitness payoffs are delayed,

Table 1
Descriptive characteristics of the Maya and Savanna Pumé study populations giving means, standard deviations and ANOVA results for group-level comparisons.

	Maya 1992			Maya 2011			Pumé 2006–2007							
Subsistence Economy	Subsistence farmers			Mixed economy			Hunter-gatherers							
Total scan observations	18,591			6288			24,922							
	Mean	SD	n	Mean	SD	n	Mean	SD	n	ANOVA Results				Total
										F	Sig	Mean	SD	n
Control & descriptive variables														
Maternal Age	30.44	6.19	9	25.18	5.26	8	27.90	9.26	10	1.11	0.35	27.94	7.31	27
Age child (years)[a]	1.90	0.67	9	1.91	0.90	8	1.61	1.03	9	1.13	0.34	1.73	0.93	27
Child weight (kg)	7.61	1.11	9	10.38	1.94	8	8.81	2.38	9	4.59	0.02	8.88	2.14	26
Main predictors														
% Allocare (direct only)[b]	0.52	0.23	9	0.43	0.22	8	0.35	0.13	10	2.00	0.16	0.43	0.20	27
Outcome variables														
Interbirth interval	2.58	0.64	7	3.73	0.54	4	2.40	1.52	5	2.36	0.13	2.81	1.07	16
Surviving fertility	7.11	1.62	9	3.13	1.36	8	2.30	1.70	10	24.36	< 0.01	4.15	2.64	27
Child weight status[c]	0.48	0.08	9	0.66	0.12	8	0.48	0.13	9	7.06	< 0.01	0.54	0.14	26

n's indicate the number of mother-infant dyads. Of the 27 mother-infant dyads across the three samples, one Savanna Pumé mother had two nursing infants (one died in 2006, and another was born later that year) and is counted as two dyads. Weight is missing for one infant, and 10 mothers had not closed the birth interval by the completion of this study (either because it was their last child or they had not yet given birth).

[a] Infant age averaged across scan sample observations.

[b] Allocare is calculated as the sum of direct care observations that an infant receives from someone other than its mother divided by the sum of all direct care observations that the infant receives (n = 5406 scan observations for 27 mother-infant dyads). 1 minus the value then gives the amount of direct care that a mother provides. As throughout, direct care is defined as intimate behaviors that imply close physical proximity and include nursing, feeding, carrying, holding, grooming (dressing, bathing, delousing, giving minor medical attention) and playing with an infant.

[c] Child's weight at time of scan sampling converted into 2006 WHO z-scores using the LMS method [87,88].

Table 2
Six models evaluating the probability that a nursing mother engages in direct care, breastfeeding or an economic activity (dependent variables) as a function of the percent of allocare (direct or indirect) her nursing infant receives (main predictor). The models control for infant age, and account for group differences and repeated observations in a nested model structure. Results shown for the main predictor only (see Table S3 supplemental materials for full model results). Models use scan observations for 27 nursing mothers.

	β	SE	Pr > |t|	95% Confidence Limit		Scan observations (n)
Direct care						
% direct allocare	−0.025	0.009	0.013	−0.045	−0.006	4878
% indirect allocare	−0.007	0.009	0.453	−0.025	0.011	4878
Breastfeeding						
% direct allocare	−0.016	0.007	0.025	−0.030	−0.002	4878
% indirect allocare	−0.001	0.006	0.920	−0.013	0.012	4878
Economic activity						
% direct allocare	0.001	0.016	0.950	−0.033	0.035	4612
% indirect allocare	0.017	0.012	0.166	−0.008	0.042	4612

Table 3
Three models evaluating interbirth interval length, surviving fertility and child weight status (dependent variables) as a function of the direct allocare a mother's nursing infant receives (main predictor), controlling for maternal age and group. Results are shown for the main predictors only (see Table S4 supplemental materials for full model results). Models use summary data for 27 mother-infant dyads.[a]

Dependent variable	β	SE	Pr > |t|	95% Confidence Limit		Mother-infant dyads (n)
Interbirth interval	−0.261	1.228	0.836	−2.997	2.474	16
Surviving fertility	1.943	1.072	0.084	−0.286	4.172	27
Child weight status	−0.014	0.014	0.329	−0.043	0.015	26

[a] Weight is missing for one infant, and 10 mothers had not closed the birth interval by the completion of this study (either because it was their last child or they had not yet given birth).

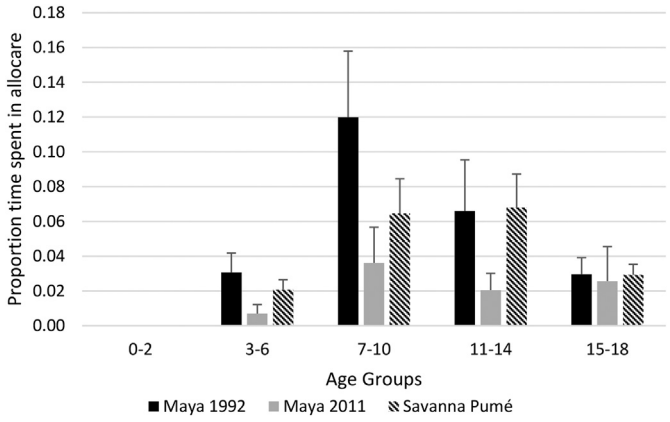


Fig. 3. Proportion of time that Maya 1992, Maya 2011 and Savanna Pumé children (bars left to right) spend providing allocare (mean and standard error).

Table 4
Eight models evaluating the proportion of time children ages 3–15 spend in work, play and education (dependent variables) as a function of the proportion of time they spend in direct childcare (main predictor), controlling for child age and sex. Results are stratified by group and shown for the main predictor only (see Table S5 supplemental materials for full model results).

	β	SE	Pr > |t|	95% Confidence Limit		Children in sample (n)
Work						
Maya 1992	0.029	0.208	0.891	−0.392	0.449	43
Maya 2011	0.475	0.409	0.256	−0.362	1.310	33
Savanna Pumé	−0.392	0.380	0.314	−1.178	0.395	27
Play						
Maya 1992	−0.662	0.299	0.034	−1.269	−0.054	43
Maya 2011	0.279	0.391	0.481	−0.521	1.078	33
Savanna Pumé	0.454	0.548	0.416	−0.680	1.587	27
Education						
Maya 1992	0.089	0.145	0.544	−0.208	0.386	43
Maya 2011	−0.501	0.344	0.157	−1.205	0.204	33

cooperation may be motived by factors other than fitness benefits [100–102].

This leads to our third finding that besides mothers, children spend the most time caretaking infants and at little cost to alternative ways that they might spend their time. While fathers, grandmothers, aunts and others help, the majority of the allocare that infants receive comes from their unmarried siblings. Specifically, in our focal groups children 7 to 14 years old allocate the most time to childcare. This age pattern of children being childcare specialists has been qualitatively noted by many ethnographers [23,93,103–107], and follows from the thesis that helping behaviors are a critical stage in child development [99]. The relative importance of child caretakers in our focal groups is consistent with what we observe in the broader cross-cultural sample (see Fig. 1). Humans are not unusual in this regard, and sibling help is common in many cooperative breeding species [2,60,108,109].

To link this common pattern to the question of why helpers help, we found children provide allocare without compromising the time they might otherwise spend in play, economic activities or education. Cross culturally, children tend to decrease the time they spend in childcare the older they are, a trend that continues until they become parents themselves. Concomitantly, the older children are, the more time they spend in economic activities or school [12,25,110]. One explanation proposed for why children are important allo-caretakers is that because subadults and adults are stronger, more skilled and more efficient at a greater range of economic tasks, the opportunity cost for them to allocate time to childcare is higher [66]. In contrast younger children have fewer competing ways to spend their time and energy. Nor are they weighing allocating effort toward mating and reproduction. We find that taking care of ones siblings is not predictive of a decrease in work or education. Ivey [11] makes a similar observation that the time opportunity costs for caretakers other than the mother were relatively low. Likewise, studies among nonhuman cooperative breeders find that although helping may incur a transient energetic cost, it has no enduring fitness cost to helpers [111–113]. While we expect specific patterns to vary cross culturally, the low opportunity cost for children to help offers an explanation why they are common caretakers in many societies, even in the absence of indirect fitness benefits.

Finally, while potential caretakers may live in a household with an infant, how much care they actually provide is variable. Among the Savanna Pumé, potential helpers (older siblings, fathers, grandmothers) allocate between 0 and 17% of their time to childcare and among the Maya between 0 and 33%. In other words, although demographically present in a household, many potential “helpers” may do nothing or they may make a considerably difference to mothers and infants. This emphasizes the importance of using behavioral data to move forward our understanding of the effects that allocare and reproductive cooperation have on a mother's time, fertility and child outcomes.

5. Conclusion

Infant care is potentially a costly form of cooperation because infants are too young to reciprocate, childcare is energetically demanding [94] and involves tasks that helpers do not otherwise do to support themselves. These costs raise the question why helpers help and to what benefit for mothers and infants. Modeling results showed that across our focal hunter-gatherer and agricultural groups 1) much of the care an infant receives comes from allo-caretakers; 2) other than mothers, siblings spend the most time caring for infants, and they do so at little cost to other ways that they might spend their time; 3) infant allocare has a significant time savings for mothers, and an implied energy savings available to reallocate to other activities besides direct care. Our results lend support to the often made observation that children specialize in childcare. These results together point to the importance of infant allocare and its immediate benefits to a mother's time budget and her ability to maintain flexibility in balancing the competing time demands to support both older and younger children.

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Appendix A. Supplementary data

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References

[1] M. Hurtado, et al., Trade-offs between female food acquisition and child care among Hiwi and Ache foragers, Hum. Nat. 3 (3) (1992) 1–28.
[2] A.F. Russell, Mammals: comparisons and contrasts, in: W.D. Koenig, J.I. Dickinson (Eds.), Ecology and Evolution of Cooperative Breeding Birds, Cambridge University Press, Cambridge, 2004, pp. 210–227.

[3] A. Cockburn, Prevalence of different modes of parental care in birds, Proc. R. Soc. B 273 (2006) 1375–1383.
[4] J.D. Ligon, D.B. Burt, Evolutionary origins, in: W.D. Koenig, J.L. Dickinson (Eds.), Ecology and Evolution of Cooperative Breeding in Birds, Cambridge University Press, Cambridge, 2004, pp. 5–34.
[5] D. Lukas, T. Clutton-Brock, Cooperative breeding and monogamy in mammalian societies, Proc. R. Soc. B 259 (2012) 2151–2156.
[6] S. Rosenbaum, L. Gettler, With a little help from her friends (and family) part I: nonmaternal caregiving behavior and physiology in mammals, Physiol. Behav. (2018) (this volume).
[7] S.B. Hrdy, Of marmosets, men and the transformative power of babies, in: W.R. Trevathan, K.R. Rosenberg (Eds.), Costly and Cute. Helpless Infants and Human Evolution, School for Advanced Research, Santa Fe, 2016, pp. 177–203.
[8] J. Lancaster, C. Lancaster, Parental investment: the hominid adaptation, in: D. Ortner (Ed.), How Humans Adapt: A Biocultural Odyssey, Smithsonian Institution Press, Washington D. C, 1983.
[9] J.M. Burkart, S.B. Hrdy, C. van Schaik, Cooperative breeding and human cognitive, Evol. Anthropol. 18 (2009) 175–186.
[10] S.B. Hrdy, Evolutionary context of human development: The cooperative breeding model, in: C.S. Carter, L. Ahnert (Eds.), Attachment and Bonding: A New Synthesis, 2005 MIT Press in cooperation with Dahlem University Press: Cambridge.
[11] P.K. Ivey, Cooperative reproduction in Ituri Forest hunter-gatherers: who cares for Efe infants? Curr. Anthropol. 41 (5) (2000) 856–866.
[12] K.L. Kramer, Cooperative breeding and its significance to the demographic success of humans, Annu. Rev. Anthropol. 39 (2010) 414–436.
[13] K.L. Kramer, E. Otárola-Castillo, When mothers need others: the impact of hominin life history evolution on cooperative breeding, J. Hum. Evol. 84 (2015) 16–24.
[14] B. Hewlett, Sexual selection and paternal investment among Aka pygmies, in: L. Betzig, M. Borgerhoff Mulder, P. Turke (Eds.), Human Reproductive Behaviour, Cambridge University Press, Cambridge, 1988, pp. 263–276.
[15] F.W. Marlowe, Who tends Hadza children? in: B.S. Hewlett, M.E. Lamb (Eds.), Hunter-Gatherer Childhoods, Aldine Transaction, New Brunswick, 2005, pp. 177–190.
[16] A.N. Crittenden, F.W. Marlowe, Allomaternal care among the Hadza of Tanzania, Hum. Nat. 19 (2008) 249–262.
[17] N. Howell, Life Histories of the Dobe !Kung, University of California Press, Berkeley, 2010.
[18] M. Konner, The Evolution of Childhood: Relationships, Emotion, Mind, Harvard University Press, 2010.
[19] C.L. Meehan, Maternal time allocation in two cooperative childrearing societies, Hum. Nat. 20 (4) (2009) 375.
[20] B. Hewlett, et al., Parental investment strategies among Aka foragers, Ngandu farmers and Euro-American urban-industrialists, in: L. Cronk, N. Chagnon, W. Irons (Eds.), Adaptation and Human Behavior: An Anthropological Perspective, Aldine de Gruyter, New York, 2000, pp. 155–178.
[21] M. Borgerhoff Mulder, M. Milton, Factors affecting infant care in the Kipsigis, J. Anthropol. Res. 41 (3) (1985) 255–260.
[22] B.A. Piperata, Variation in maternal strategies during lactation: the role of the biosocial context, Am. J. Hum. Biol. 21 (6) (2009) 817–827.
[23] R. Hames, The allocation of parental care among the Ye'Kawana, in: L. Betzig, M. Borgerhoff Mulder, P. Turke (Eds.), Human Reproductive Behavior, Cambridge University Press, Cambridge, 1988, pp. 237–251.
[24] M. Hurtado, et al., Female subsistence strategies among Ache hunter-gatherers of eastern Paraguay, Hum. Ecol. 13 (1985) 1–28.
[25] K.L. Kramer, Does it take a family to raise a child? in: G. Bentley, R. Mace (Eds.), Substitute Parents. Biological and Social Perspectives on Alloparenting in Human Societies, Berghahn Books, New York, 2009, pp. 77–99.
[26] K. Hawkes, J. O'Connell, N. Blurton Jones, Hadza women's time allocation, offspring provisioning and the evolution of long postmenopausal life spans, Curr. Anthropol. 38 (4) (1997) 551–577.
[27] J.D. Wray, Maternal nutrition, breast-feeding and infant survival, Nutrition and Human Reproduction, 1978, pp. 197–229.
[28] K.L. Kramer, The evolution of human parental care and recruitment of juvenile help, Trends Ecol. Evol. 26 (10) (2011) 533–540.
[29] N. Blurton Jones, K. Hawkes, P. Draper, Foraging returns of !Kung adults and children: why didn't !Kung children forage? J. Anthropol. Res. 50 (3) (1994) 217–248.
[30] A.N. Crittenden, et al., Juvenile foraging among the Hadza: implications for human life history, Evol. Hum. Behav. 34 (2013) 299–304.
[31] K. Hawkes, J. O'Connell, N. Blurton Jones, Hadza children's foraging: juvenile dependency, social arrangements, and mobility among hunter-gatherers, Curr. Anthropol. 36 (4) (1995) 688–700.
[32] K.L. Kramer, Maya Children: Helpers at the Farm, Harvard University Press, Cambridge, 2005.
[33] K.L. Kramer, Why what juveniles do matters in the evolution of cooperative breeding, Hum. Nat. 25 (1) (2014) 49–65.
[34] B. Tucker, A. Young, Growing up Mikea. Children's time allocation and tuber foraging in southwest Madagascar, in: B.S. Hewlett, M.E. Lamb (Eds.), Hunter-Gatherer Children, Aldine Transaction, New Brunswick, 2005, pp. 147–171.
[35] N. Blurton Jones, K. Hawkes, J. O'Connell, Measuring and modeling costs of children in two foraging societies: implications for schedule of reproduction, in: V. Standen, R. Foley (Eds.), Comparative Socioecology. The Behavorial Ecology of Humans and Other Mammals, Blackwell Scientific Publications, Oxford, 1989, pp. 367–390.
[36] R.B. Lee, The !Kung San: Men, Women and Work in a Foraging Society, Cambridge University Press, Cambridge, 1979.
[37] R. Sullivan Robinson, R. Lee, K. Kramer, Counting women's labor: a reanalysis of children's net productivity in Mead Cain's Bangladeshi village, Popul. Stud. 62 (1) (2008) 25–38.
[38] K.L. Kramer, P.T. Ellison, Pooled energy budgets: resituating human energy allocation tradeoffs, Evol. Anthropol. 19 (2010) 136–147.
[39] L.A. Fairbanks, Juvenile vervet monkeys: establishing relationships and practicing skills for the future, in: M.E. Pereira, L.A. Fairbanks (Eds.), Juvenile primates: Life history, development, and behavior, Oxford University Press, Oxford, 1993, pp. 211–227.
[40] S.B. Hrdy, Care and exploitation of nonhuman primate infants by conspecifics other than the mother, Adv. Study Behav. 6 (1976) 101–158.
[41] S.B. Hrdy, Mother Nature, Pantheon Books, New York, 1999.
[42] J. Lancaster, Play mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (Cercopithicus aethiops), Folia Primatol. 15 (1971) 161–182.
[43] J.J. McKenna, Parental supplements and surrogates among primates: cross-species and cross-cultural comparisons, in: J. Lancaster, et al. (Ed.), Parenting Across the Life Span, Aldine de Gruyter, New York, 1987, pp. 143–184.
[44] S.D. Tardif, The bioenergetics of parental care in marmosets and tamarins, in: N.G. Solomon, J.A. French (Eds.), Cooperative Breeding in Mammals, Cambridge University Press, Cambridge, 1997, pp. 11–33.
[45] A.L. Salo, J.A. French, Early experience, reproductive success, and development of parental behaviour in Mongolian gerbils, Anim. Behav. 38 (4) (1989) 693–702.
[46] L. Fairbanks, Reciprocal benefits of allomothering for female vervet monkeys, Anim. Behav. 40 (1990) 553–562.
[47] K.L. Kramer, A. Veile, E. Otárola-Castillo, Sibling competition, growth tradeoffs. Biological vs. statistical significance, PLoS One 11 (3) (2016) e0150126.
[48] W.D. Hamilton, The genetical evolution of social behavior, I and II, J. Theor. Biol. 9 (1964) 12–45.
[49] J.J. Boomsma, Lifetime monogamy and the evolution of eusociality, Philos. Trans. R. Soc. B 364 (2009) 3191–3207.
[50] M. Briga, I. Pen, J. Wright, Care for kin: within-group relatedness and allomaternal care are positively correlated and conserved throughout the mammalian phylogeny, Biol. Lett. 8 (2012) 533–536.
[51] L.E. Browning, et al., Kin selection, not group augmentation, predicts helping in an obligate cooperative breeding bird, Proc. R. Soc. B 279 (2012) 3861–3869.
[52] A. Cockburn, Evolution of helping behavior in cooperatively breeding birds, Annu. Rev. Ecol. Syst. 29 (1998) 141–177.
[53] W.O.H. Hughes, et al., Ancestral monogamy shows kin selection in key to the evolution of eusociality, Science 320 (2008) 1213–1216.
[54] A.F. Russell, B.J. Hatchwell, Experimental evidence for kin-baised helping in a cooperatively breeding vertebrate, Proc. R. Soc. B 268 (2001) 2169–2174.
[55] S.T. Emlen, Evolution of cooperative breeding in birds and mammals, in: J.R. Krebs, N.B. Davies (Eds.), Behavioral Ecology. An Evolutionary Approach, Third Edition, Blackwell Scientific Publications, London, 1991, pp. 301–337 (1978).
[56] W. Koenig, R. Mumme, Levels of analysis, functional explanations, and the significance of helper behavior, in: M. Bekoff, D. Jamieson (Eds.), Interpretation and Explanation in the Study of Animal Behavior, vol. 1, Westview Press, Boulder, 1991, pp. 268–303.
[57] A.F. Skutch, Helpers at Birds' Nests. A Worldwide Survey of Cooperative Breeding and Related Behavior, University of Iowa Press, Iowa City, 1987.
[58] K.G. Anderson, Relatedness and investment in children in South Africa, Hum. Nat. 16 (2005) 1–31.
[59] R. Bergmüller, et al., Integrating cooperative breeding into theoretical concepts of cooperation, Behav. Process. 76 (2) (2007) 61–72.
[60] T.H. Clutton-Brock, Breeding together: kin selection and mutualism in cooperative vertebrates, Science 296 (2002) 69–72.
[61] T.H. Clutton-Brock, et al., Contributions to cooperative rearing in meerkats, Anim. Behav. 61 (2001) 705–710.
[62] A.S. Griffin, S.A. West, Kin selection: fact and fiction, Trends Ecol. Evol. 17 (1) (2002) 15–21.
[63] J.L. Brown, Helping and Communal Breeding in Birds, Princeton University Press, Princeton, 1987.
[64] H. Kokko, R.A. Johnstone, T.H. Clutton-Brock, The evolution of cooperative breeding through group augmentation, Proc. R. Soc. B 268 (2001) 187–196.
[65] A.E. Pusey, C. Packer, The evolution of sex-biased dispersal in lions, Behaviour 101 (4) (1987) 275–310.
[66] J. Bock, Learning, life history and productivity: children's lives in the Okavango Delta, Botswana, Human Nat. 13 (2) (2002) 161–197.
[67] K.L. Kramer, Variation in juvenile dependence: helping behavior among Maya children, Hum. Nat. 13 (2) (2002) 299–325.
[68] R.D. Greaves, K.L. Kramer, Hunter-gatherer use of wild plants and domesticates: archaeological implications for mixed economies before agricultural intensification, J. Archaeol. Sci. 41 (2013) 263–271.
[69] K.L. Kramer, R.D. Greaves, Diversity or Replace. What happens to wild foods when cultigens are introduced into hunter-gatherer diets, in: B. Codding, K.L. Kramer (Eds.), Why Forage? Hunters and Gatherers Living in the 21st Century, School of Advanced Research, Santa Fe, 2016, pp. 15–42.
[70] K.L. Kramer, Early sexual maturity among Pumé foragers of Venezuela. Fitness implications of teen motherhood, Am. J. Phys. Anthropol. 136 (3) (2008) 338–350.
[71] K.L. Kramer, R. Schacht, A. Bell, Adult sex ratios & partner scarcity among hunter-gatherers: implications for dispersal patterns and the evolution of human sociality,

Philos. Trans. R. Soc. B 372 (2017).
[72] K.L. Kramer, R.D. Greaves, Changing patterns of infant mortality and fertility among Pumé foragers and horticulturalists, Am. Anthropol. 109 (4) (2007) 713–726.
[73] E. Cashdan, et al., Mobility and navigation among the Yucatec Maya. Sex differences reflect parental investment, not mating competition, Hum. Nat. 27 (2016) 35–50.
[74] K.L. Kramer, G.P. McMillan, The effect of labor saving technology on longitudinal fertility changes, Curr. Anthropol. 47 (1) (2006) 165–172.
[75] A. Veile, K.K. L., Pregnancy, birth and babies: motherhood and modernization in a Yucatec village, in: D.A. Schwartz (Ed.), Maternal Health, Pregnancy-Related Morbidity and Death Among Indigenous Women of Mexico & Central America, Springer Press, 2017.
[76] A. Veile, K.L. Kramer, Birth and breastfeeding dynamics in a modernizing indigenous community, J. Hum. Lact. 5 (2014) 1–11.
[77] A. Veile, et al., Modernization is associated with intensive breastfeeding patterns in the Bolivian Amazon, Soc. Sci. Med. 100 (2014) 148–158.
[78] G.E. Kennedy, From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context, J. Hum. Evol. 48 (2005) 123–145.
[79] J. Altmann, Observational study of behavior: sampling methods, Behaviour 49 (3) (1974) 227–266.
[80] M. Borgerhoff Mulder, T.M. Caro, The use of quantitative observational techniques in anthropology, Curr. Anthropol. 26 (1985) 323–335.
[81] R. Hames, Time allocation, in: E.A. Smith, B. Winterhalder (Eds.), Evolutionary Ecology and Human Behavior, Aldine De Gruyter, New York, 1992, pp. 203–235.
[82] R.I.M. Dunbar, Some aspects of research design and their implications in the observational study of behaviour, Behaviour 58 (1–2) (1976) 58–78.
[83] M. Simpson, A. Simpson, One-zero and scan methods for sampling behaviour, Anim. Behav. 25 (1977) 726–731.
[84] P. Reynolds, Dance Civet Cat. Child Labour in the Zambezi Valley, Ohio University Press, Athens, 1991.
[85] T.G. Lohman, A.F. Roche, R. Martorell (Eds.), Anthropometric Standardization Reference Manual, Human Kinetics Books, Champaign, IL, 1988.
[86] D.G. Kleiman, J.R. Malcolm, The evolution of male parental investment in mammals, Parental Care in Mammals, Springer, 1981, pp. 347–387.
[87] T.J. Cole, P.J. Green, Smoothing reference centile curves: the LMS method and penalized likelihood, Stat. Med. 11 (1992) 1305–1319.
[88] WHO Multicentre Growth Reference Study Group, WHO Child Growth Standards: Length/Height-for-Age, Weight-for-Age, Weight-for-Length, Weight-for-Height and Body Mass Index-for-Age: Methods and Development, World Health Organization, Geneva, 2006.
[89] K. Hill, A.M. Hurtado, Ache Life History, Aldine de Gruyter, New York, 1996.
[90] N. Howell, Demography of the Dobe !Kung, Academic Press, New York, 2000 (1979).
[91] R.D. Greaves, Ethnoarchaeological Investigation of Subsistence Mobility, Resource Targeting, and Technological Organization among Pumé Foragers of Venezuela, Ph.D. dissertation University of New Mexico, Albuquerque, 1997.
[92] K.L. Kramer, R.D. Greaves, Synchrony between growth and reproductive patterns in human females: rapid juvenile growth among Pumé foragers, Am. J. Phys. Anthropol. 141 (2) (2010) 235–244.
[93] C.R. Valeggia, Flexible caretakers. Responses of Toba families in transition, in: G. Bentley, R. Mace (Eds.), Substitute Parents. Biological and Social Perspectives on Alloparenting in Human Societies, Berghahn Press, New York, 2009, pp. 100–114.
[94] C.L. Meehan, R. Quinlan, C.D. Malcom, Cooperative breeding and maternal energy expenditure among Aka foragers, Am. J. Hum. Biol. 25 (2013) 42–57.
[95] S. Ulijaszek, Human Energetics in Biological Anthropology, Cambridge University Press, Cambridge, 1995.
[96] D.W. Sellen, D.B. Smay, Relationship between subsistence and age at weaning in "preindustrial" societies, Hum. Nat. 12 (1) (2001) 47–87.
[97] A. Veile, K.L. Kramer, Shifting weanling's optimum: breastfeeding ecology and infant health in Yucatan, in: C. Tomori, A.E.L. Palmquist, E. Quinn (Eds.), Anthropology and Breastfeeding, Routledge Press, 2018(Chapter 12).
[98] M. Konner, Hunter-gatherer infancy and childhood, in: B.S. Hewlett, M.E. Lamb (Eds.), Hunter-Gatherer Childhoods: Evolutionary, Developmental and Cultural Perspectives, ALdine Transaction, New Brunswick, 2005.
[99] D. Lancy, Anthropological Perspectives on Children as Helpers, Workers, Artisans, and Laborers, Springer Nature Press, New York, 2018.
[100] D.A. Coall, R. Hertwig, Grandparental investment: past, present, and future, Behav. Brian Sci. 33 (2010) 1–59.
[101] F. de Waal, Putting the altruism back into altruism: the evolution of empathy, Annu. Rev. Psychol. 59 (2008) 279–300.
[102] J. Silk, Nepotistic cooperation in non-human primate groups, Philos. Trans. R. Soc. B 364 (2009) 3243–3254.
[103] H. Barry, L.M. Paxson, Infancy and early childhood: cross-cultural codes 2, Ethnology 10 (4) (1971) 466–508.
[104] M.V. Flinn, Parent-offspring interactions in a Caribbean village: daughter guarding, in: L. Betzig, M. Borgerhoff Mulder, P. Turke (Eds.), Human Reproductive Behavior: A Darwinian Perspective, Cambridge University Press, Cambridge, 1988, pp. 189–200.
[105] M. Nag, B. White, R. Peet, An anthropological approach to the study of the economic value of children in Java and Nepal, Curr. Anthropol. 19 (2) (1978) 293–306.
[106] T. Weisner, R. Gallimore, My brother's keeper: child and sibling caretaking, Curr. Anthropol. 18 (1977) 169–190.
[107] B.B. Whiting, C.P. Edwards, Children of Different Worlds. The Formation of Social Behavior, Harvard University Press, Cambridge, 1988.
[108] T.H. Clutton-Brock, Structure and function in mammalian societies, Philos. Trans. R. Soc. B 364 (2009) 3229–3242.
[109] J.S. Gilchrist, A.F. Russell, Who cares? Individual contributions to pup care by breeders vs non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*), Behav. Ecol. Sociobiol. 61 (2007) 1053–1060.
[110] E. Schniter, et al., Skill ontogeny among Tsimane forager-horticulturalists, Am. J. Phys. Anthropol. 158 (1) (2015) 3–18.
[111] T. Clutton-Brock, M. Manser, Meerkats: cooperative breeding in the Kalahari, in: W.D. Koenig, J.L. Dickinson (Eds.), Cooperative Breeding in Vertebrates, Cambridge University Press, Cambridge, 2016, pp. 294–317.
[112] T.H. Clutton-Brock, Cooperative breeding in mammals, in: P.M. Kappeler, C.P. van Schaik (Eds.), Cooperation in Primates and Humans, Springer-Verlag, Berlin, 2006, pp. 173–190.
[113] A.F. Russell, et al., Cost minimization by helpers in cooperative vertebrates, Proc. Natl. Acad. Sci. 100 (6) (2003) 3333–3338.
[114] W.W. Denham, Infant Transport Among the Alyawara Tribe, Central Australia. Oceania, 64(4) (1974), pp. 253–277.
[115] M. Goodman, et al., The comparability of hunting and mothering among the Agta humer-gatherers of the Philippines, Sex Roles 12 (1985) 1199–1209.
[116] K.L. Kramer, Children's help and the pace of reproduction: cooperative breeding in humans, Evol. Anthropol. 14 (6) (2005) 224–237.
[117] M.V. Flinn, Paternal care in a Caribbean village, in: B. Hewlett (Ed.), Father-Child Relations, Aldine de Gruyter, New York, 1992, pp. 57–84.