

Allomaternal Care among the Hadza of Tanzania

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Abstract Cooperative child care among humans, where individuals other than the biological mother (allomothers) provide care, may increase a mother's fertility and the survivorship of her children. Although the potential benefits to the mother are clear, the motivations for allomothers to provide care are less clear. Here, we evaluate the kin selection allomothering hypothesis using observations on Hadza hunter-gatherers collected in ten camps over 17 months. Our results indicate that related allomothers spend the largest percentage of time holding children. The higher the degree of relatedness among kin, the more time they spend holding, supporting the hypothesis of nepotism as the strongest motivation for providing allomaternal care. Unrelated helpers of all ages also provide a substantial amount of investment, which may be motivated by learning to mother, reciprocity, or coercion.

Keywords Allomothers · Child care · Cooperative breeding · Hadza · Hunter-gatherers · Kin selection

Direct care or provisioning of young by individuals other than the biological parents (alloparenting) exists in many species of insects and birds, as well as some mammals (Asa 1997; Cockburn 1998; Emlen 1994; French 1997; Garber and Leigh 1997; Heinsohn and Double 2004; Jarvis et al. 1994; Wilson 1971). Pair bonds are absent in most primate species and mothers provide the bulk of caretaking, though in several species allomothers may also provide extensive care. Across human populations, mothers routinely rely on the support of allomothers to help provision

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and nurture their offspring (Bove et al. 2002; Hawkes et al. 1997; Hrdy 2005a; Ivey 2000; Kramer 2005; Meehan 2005). Human females are unique among apes in that their infants are weaned well before they are nutritionally independent. This allows mothers to resume ovulation sooner and have subsequent offspring more rapidly, shortening the inter-birth interval (IBI) (Hawkes 1997; Hawkes et al. 1998). Contribution of care by allomothers can have a positive effect on a mother's fertility and/or the survivorship of her children (Berezkei and Dunbar 1997, 2002; Crognier et al. 2001, 2002; Flinn 1989; Ivey 2000; Sear et al. 2000, 2002; Turke 1988). While the potential benefits of cooperative care from the mother's perspective are clear, the motivation for allomothers to provide assistance is more difficult to explain.

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

For humans, among whom a wide range of adult, subadult, related, and unrelated helpers contribute care, the costs and benefits of helping may involve various tradeoffs depending on the age and reproductive status of the caregiver (Kramer 2005). Helping is facultative, and if the cost of helping is too high, allomothers may not provide care (Hrdy 2005b). When allomothers can gain from helping kin, we should expect that (all else being equal) their investment will be greater when the degree of relatedness to the recipient child is higher. A handful of studies have found a correlation between the degree of genetic relatedness and the amount of care provided in some human populations (Denham 1974; Hames 1988; Ivey 2000).

The current study uses data on allomothering to test the kin selection hypothesis among the Hadza foragers of Tanzania. Previous analyses have shown that although Hadza mothers spend the most time in direct child care, children also receive a considerable amount of care from a wide range of helpers (Marlowe 2005). Given that humans have pair bonds, fathers may be a special category of helper. Here, however, we use the term "allomother" rather than "alloparent" to be consistent with much of the literature on other species, and because mothers are clearly the primary caretaker in most, if not all, human societies.

In addition to Hadza fathers (Marlowe 1999, 2003), Hadza grandmothers do a considerable amount of caretaking (Hawkes et al. 1989, 1997). Grandmothers and fathers are important allomothers, providing both direct care, such as holding, and indirect care, such as provisioning (Marlowe 2005). However, many others also provide allomaternal care. We focus here on holding as an indicator of direct care. Our aim is to identify the constellation of caregivers, evaluate how much time they spend holding, and determine which categories of caregivers are holding the most, and why.

The Hadza

The Hadza are hunter-gatherers who live in a savanna-woodland habitat in northern Tanzania; their population numbers approximately 1,000. They live in camps with an average of 30 individuals, but camp composition is fluid and people often move in and out. Camps are moved every month or two, mainly in response to the seasonal availability of water and foods (Marlowe 1999; Woodburn 1968). Serial monogamy is the best way to describe the Hadza mating system. Divorce and remarriage are common; consequently, stepchildren and stepfathers are also common (Blurton Jones et al. 2000). Kinship is traced bilaterally (Woodburn 1968) and although both men and women value living with their mothers, there is a bias toward living with the wife's kin; 60–70% of married couples live with the wife's family (Blurton Jones et al. 2005; Marlowe 2004; Woodburn 1968).

Men usually forage alone, collecting baobab fruit and several types of honey, as well as hunting a wide variety of birds and mammals. Hadza women forage in groups, collecting baobab fruit and berries and digging up underground tubers. Nursing infants accompany their mothers on daily foraging trips, but when a child is approximately 2–3 years old and being weaned, they are typically left in camp with others. Children may be left without adult supervision but in that case are typically under the charge of at least one teenager.

Young children are raised in a communal setting. In camp, children often play while their mothers process food, such as the baobab, which is pounded into a powder and mixed with water to make a paste that is an important weaning food. Children's play includes games, dolls made out of mud or cloth, and target practice, but it often takes the form of digging tubers as well (Blurton Jones 1993). Children spend a considerable amount of time foraging and tend to focus on easy-to-collect foods that are located close to camp (Blurton Jones 1993); they may be acquiring up to 50% of their daily caloric intake by age 10 (Blurton Jones et al. 1989). In addition to foraging for their own consumption, they also provision their younger siblings or other younger children left in their charge.

Methods

The current study expands on a previous report by Marlowe (2005). Here we use a considerably larger sample of subadults as well as adult allomothers and control for residence/non-residence in camp for each category of helper. Data were collected in ten camps over 17 months of fieldwork from 1995 to 2004. Holding was measured by conducting hourly instantaneous scan observations from sunrise to sunset (13 per day) in which the behavior of every individual in camp was recorded. We analyzed holding (from the holder's perspective) and being held (from the child's perspective). When we refer to "being held," the unit of analysis is the child; when we say "holding," the unit of analysis is the allomother. Although holding/being held does not offer a complete picture of cooperative care, it is an easily quantifiable behavior that can be energetically demanding (Kramer 1998; Mitani and Watts 1997), as well as being essential in keeping infants from hurting themselves—for example, by falling or getting burned in a hearth.

It is very rare for children over 4 years of age to be routinely held because they are heavy and fairly independent. For this reason, only children 4 years of age and younger are used here. Holders younger than 18 were designated as “subadults” and holders older than 18 were designated as adults. The behavior of all individuals present in camp during a camp scan was recorded. Although 13 scans were performed daily, there was considerable variability in the number of scans conducted per camp and thus per individual. Large camps required longer stays in order to collect other data. There was also variation in the amount of time people were residing in a camp as well as in the number of scans in which they appeared, owing to how much time they were out of camp foraging.

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

We also analyzed counts of observations of holding/being held using nonparametric tests, weighting more heavily the cases for which the number of observations was greater (see [Appendix](#)). In every instance our results were confirmed. The analysis presented here has the advantage of allowing us to control for the age of the child.

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

Eighteen relationship categories were initially coded for analyzing holding behavior (relationship between holder and holdee). These included mother; father; maternal and paternal grandparents, aunts, uncles, and cousins; distantly related kin; and unrelated individuals. Only biological fathers were coded as “father”—stepfathers were coded as unrelated. An individual was classified as a “distant relative” if they were more distantly related than first cousin. To make categories more manageable for the initial descriptive statistics, the relationships that accounted for <1% of the time a child was being held were assigned to the category “other kin,” which include maternal and paternal grandfathers, paternal aunt, maternal and paternal cousins, and distant relatives. A 0.5 degree of relatedness includes fathers and siblings; 0.25 includes grandparents, half-siblings, aunts, and uncles; and 0.125 includes cousins. Proportions of time a child was held by categories of all persons with each degree of relatedness were also determined. All holding by mothers, including holds when the mother was nursing, were included in the initial descriptive analyses. However, because the aim of this study is to determine the extent of allomaternal care, we excluded holding by mother in all subsequent analyses.

We controlled for the residence of the allomother in the following comparisons: when determining if being held was a product of kin selection (comparison of time being held by degrees of relatedness), maternal versus paternal kin, and maternal grandmothers versus paternal grandmothers. When determining if the degree of

relatedness between holder and child correlated with the amount of time a child was held, only children who had at least one representative from each category of relatedness (0.5, 0.25, and 0.125) living in camp were included. In order to control for residence of maternal and paternal kin, we only included children who had at least two maternal and paternal kin members living in camp.

We used a multivariate linear regression model that controlled for the age and sex of the child when determining if the three categories of degree of relatedness to the child decreasingly (from 0.5 to 0.125) predicted proportions of time being held. For these, we report standardized betas. The Wilcoxon signed rank test for related samples was used when the child being held was the unit of analysis. For example, we used the Wilcoxon signed rank to test whether children were held more by all kin than all non-kin, or by all maternal kin than all paternal kin, or by the maternal grandmother than the paternal grandmother. Mann-Whitney *U* tests were used when the unit of analysis was the holder—for example, to test whether female allomothers held more than male allomothers.

Results

A total of 470 individuals ($n_1=234$ females, $n_2=236$ males) were represented in 42,031 person scans. The sample included 68 children who were 4 years old and younger ($n_1=28$ females, $n_2=40$ males), of which 74% were held ($n_1=25$ females, $n_2=31$ males); all children 4 years of age or younger were included in the analyses, whether they were observed being held or not. A total of 185 individuals were observed holding ($n_1=132$ females, $n_2=53$ males); 46 were mothers and 139 were allomothers. Of the total time Hadza children were held, 69% of the time they were held by their mother and 31% by allomothers (Table 1), who ranged in age from 1.5 to 79 years old.

A child's age is, of course, a strong and significant predictor of the proportion of time he/she is held, with younger children being held more ($\beta=-0.762$, $p<0.0005$,

Table 1 Percentage of the total time (100%) that children ≤ 4 years of age ($n=68$) were being held by all caregivers

Relationship category	<i>n</i>	Mean percent of time being held	Mean percent of time being held controlling for residency in camp
Mother	46	68.7	68.9
Father	34	7.1	9.4
Older sister	56	1.2	2.8
Maternal grandmother	16	3.7	9.5
Paternal grandmother	8	1.2	6.1
Maternal aunt	33	1.9	3.5
Other kin	^a	3.6	^a
Unrelated	77	12.4	^a
Total	–	100	100

^a“Other kin” represents various categories of helpers. Because individuals may fall in more than one category, the *n* is not known. Residence could not be controlled for the “other kin” and “unrelated” categories because they overlap

df=66, $R^2=0.575$, $n_1=28$ females, $n_2=40$ males) (Fig. 1). For this reason, child's age is controlled in all tests where the child is the unit of analysis. The sex of a child (males=1, females=2) was not associated with the proportion of time a child was held ($\beta=0.040$, $p=0.747$, df=66, $R^2=-0.014$, $n_1=28$ females, $n_2=40$ males).

Across holders of all ages, females spent more time holding children than males (Fig. 2), but the difference was not quite significant (Mann-Whitney $U=1862.00$, $p=0.080$, $n_1=52$ males and $n_2=87$ females). Subadults age 1.5–17.9 years represented 62% of the total allomothers ($n_1=44$ females, $n_2=12$ males) (Fig. 3; the lines show locally weighted averages smoothed with a Lowess fit). Female subadult allomothers far outnumbered their male counterparts and spent a significantly greater proportion of their time holding (Mann-Whitney $U=130.5$, $p=0.008$, $n_1=44$ females, $n_2=12$ males). Figure 3 reveals that holding by girls is highest between 8 and 12 years of age.

Children were held by related allomothers (all kin, including distantly related) significantly more than by unrelated allomothers (Wilcoxon signed rank $Z=-2.439$, $p=0.015$, $n_1=62$ related, $n_2=77$ unrelated). In order to determine if categories of degree of relatedness (all holding by relatives with that degree of relatedness lumped together) between the holder and the child were significant predictors of percent time being held, we ran a multiple linear regression controlling for the age and sex of the child. We used the total proportion of time the child was held as the dependent variable and excluded all holding done by mothers. The three categories of degree of relatedness between the holder and the child were all significant but decreasingly strong predictors of percent time being held (0.5, $\beta=0.784$, $p<0.005$; 0.25, $\beta=0.489$, $p<0.005$; and 0.125, $\beta=0.127$, $p<0.005$; final model, df=67, $R^2=0.980$, $p<0.005$). Figure 4 also shows that a higher degree of relatedness between the holders and the child associates with a higher mean percent time being held.

Fig. 1 Percent of time children ≤ 4 years of age were being held

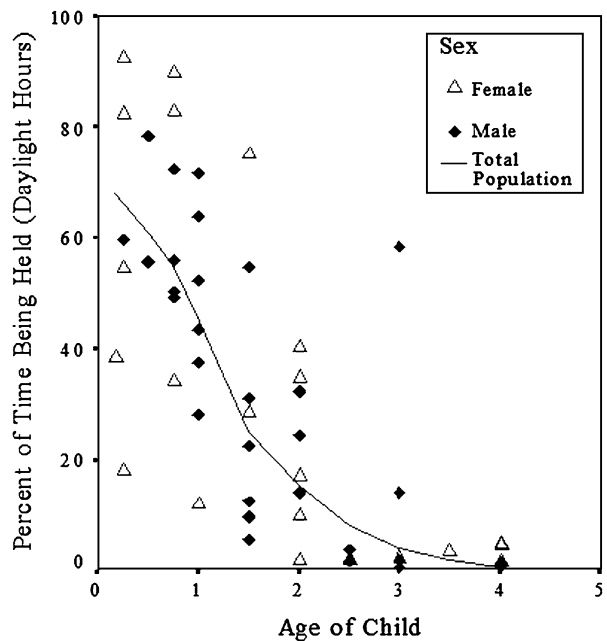
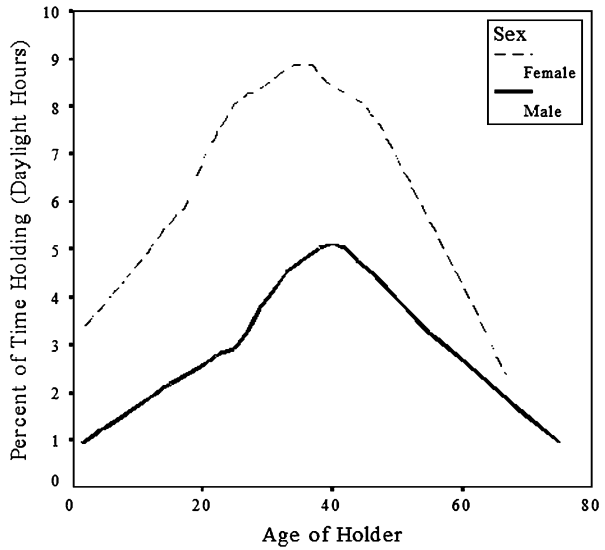


Fig. 2 Percent of time spent holding children ≤ 4 years of age (including mothers)



Although related individuals spent more time holding, children were held overall by unrelated helpers 12.4% of the time. This is more than any other single category of allomother (Table 1). Among unrelated helpers ($n_1=65$ females, $n_2=12$ males) there was no significant difference between adults and subadults in the amount of time spent holding (Mann-Whitney $U=1670.5$, $p=0.185$, $n_1=28$ subadults, $n_2=49$ adults).

Children were held more by maternal relatives than paternal relatives when residency in camp was controlled (Wilcoxon signed rank $Z=-2.808$, $p=0.005$, $n_1=78$ maternal kin, $n_2=46$ paternal kin). However, maternal grandmothers did not hold

Fig. 3 Percent of time spent holding by subadult allomothers

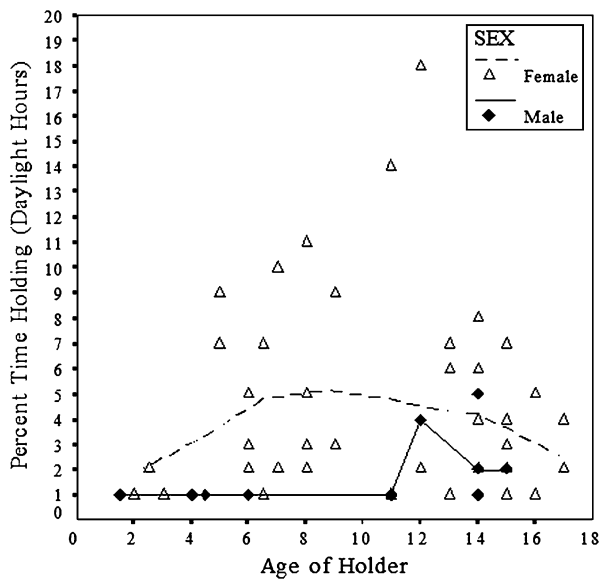
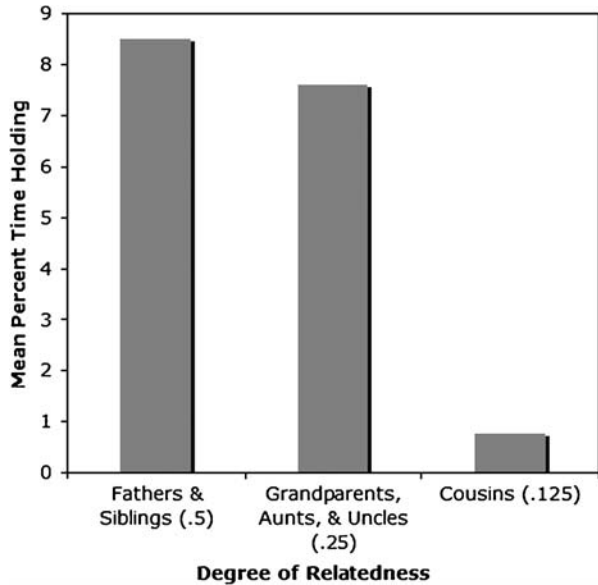


Fig. 4 Mean percent of time spent holding by allomothers by degree of relatedness to the child



significantly more than paternal grandmothers (Wilcoxon signed rank $Z=-1.079$, $p=0.281$, $n_1=28$ maternal grandmothers, $n_2=11$ paternal grandmothers). Camp residence for grandmothers is biased in that paternal grandmothers only tend to live with their grandchildren when their son is still married to the child's mother whereas maternal grandmothers are much more likely to live with their grandchildren when the father (the daughter's husband) does not still live with the child. The residence of fathers and maternal grandmothers was inversely related (Spearman's rank correlation $r_s=-0.400$, $p<0.005$, $n=68$ children), whereas the residence of fathers and paternal grandmothers was positively related (Spearman's rank correlation $r_s=0.259$, $p=0.027$, $n=68$ children).

Discussion and Conclusion

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

Both fathers and maternal grandmothers provide a substantial amount of allocare. Residence patterns in this study support previous research suggesting that a woman

will depend more on her mother when her husband is absent, and vice versa (Blurton Jones et al. 2005; Marlowe 2005). Hadza couples more frequently reside with the wife's kin (Blurton Jones et al. 2005; Woodburn 1968), and a higher number of maternal relatives appear to be routinely available to provide care. When maternal and paternal kin are compared, maternal relatives hold more frequently. However, this does not extend to grandmothers; when both are in residence there is no significant difference between the amount of time maternal and paternal grandmothers spend holding their grandchild.

Maternal grandmothers have been shown to positively affect outcomes such as survivorship and growth for their grandchildren (Berezkei 1998; Hawkes 1997; Hawkes et al. 1989; Leonetti et al. 2002, 2005; Mace and Sear 2005). Conversely, paternal grandmothers are expected to invest less than maternal grandmothers—a reflection of paternity certainty being lower than maternity certainty (Euler and Weitzel 1996). The current study shows no difference in grandmaternal frequency of holding. This suggests that the Hadza may have high paternity confidence or that paternal grandmothers may choose to live with particular sons who are more likely to have high paternity confidence. The tendency for older women to reside in the same camp with their daughters more often than with their sons could be partially influenced by maternity confidence in their daughters' children.

Related allomothers spend significantly more time holding children when compared with unrelated helpers. Relatives contribute care in proportion to their degree of relatedness to the recipient child; holding frequency is greater when the degree of relatedness to the recipient child is higher. Although the results are significant, suggesting that among the Hadza, nepotism is a primary motivation for providing allomaternal care, a causal relationship between relatedness and level of care is not necessarily confirmed. Investment from kin may derive from the fact that kin tend to co-reside, which creates the opportunity for helping (Griffin and West 2002). Of course, we should not discount the probability that kin co-residence itself is favored by kin selection (Foster et al. 2006).

Owing to the varying and often unobserved costs and benefits of providing care, it remains difficult to make strong predictions about how care will be distributed. Depending on the reproductive status of the helper, the costs and benefits will change (Kramer 2005). In addition, the costs of helping (or what are perceived as costs) may be inflated, particularly when the benefits are extremely high (Clutton-Brock 2002). For an adult, the cost of carrying an infant may be quite low when walking over short distances at slow speeds (Wall-Scheffler et al. 2007). Here, we report data on very young allomothers holding other children, and the costs of holding a 1-year-old child might be quite high for a 4-year-old allomother. The limitations of applying the kin selection hypothesis notwithstanding, the evidence provided in the current study suggests that nepotism is a factor influencing the amount of care provided. The goal of future studies will be to quantify the costs and benefits of kin investment and situate it within the larger framework of human cooperative care, including help provided by unrelated individuals.

Motivations for unrelated helpers to provide allomaternal care may include learning to mother, reciprocity, and coercion. Primates tend to be attracted to infants and to have a strong desire to touch, hold, and interact with them (Hrdy 2005a, b). Practice in child rearing may increase the reproductive success of the caregiver who

is “learning to mother” (Lancaster 1971; McKenna 1987). Subadult helpers ranging from 1.5 to 17.9 years old provide a substantial amount of care and may spend up to 20% of their time in camp holding both related and unrelated children. The very young allomothers (1.5 years) are being supervised and minded by older allomothers. Unrelated subadults may be providing care to gain practice in child rearing or may simply be exploited for their labor (coercion). For instance, a Hadza mother was witnessed (by ANC) tying her infant in a sling to a protesting, unrelated young girl. Although the unrelated helper was objecting, the mother reprimanded the girl and walked away, leaving the child with no other choice but to provide care to the infant or face the consequences. There may be penalties for not helping (Hrdy 2005a, b), making it in the best interest of the subadult allomother to help.

Helping by unrelated caregivers may also be explained by in-kind reciprocity (taking turns providing care) or not-in-kind reciprocity (trading direct care for provisioning) (Cockburn 1998; Davies 1992; Emlen 1994; Ligon and Ligon 1978). For instance, one woman may hold another woman’s child while she is out foraging and be compensated with food upon the woman’s return. Alternatively, one mother might stay in camp one day and watch the children, and on another day the second mother will stay in camp to watch the children. The social status of the recipient mother might also influence an allomother’s motivation to provide care. If a woman has a reputation as the best tuber digger and is a preferred person to live with because she provides considerable amounts of food, others may repay her by holding her children or grandchildren. Future research will explore the possible relationship between a mother’s tuber digging reputation and the reciprocal exchange between a mother and her allomaternal assistants.

Hadza mothers have access to a wide range of allomothers, allowing us to focus beyond paternal and grandmaternal investment. Nepotistic cooperation appears to be the primary motive for allomothering among the Hadza. The motive for providing care to genetically related individuals is straightforward, yet motives for providing substantial care to unrelated children remain less clear. Quantifying the costs and benefits of providing care will become less difficult using longitudinal data over many years. Future research will track dyadic holding interactions and explore how a Hadza mother’s time spent working (e.g., food processing) and/or foraging return rates are affected by allomothers, whether we see evidence of turn-taking in child care, and whether females who spend more time holding as girls become more successful mothers. We will also explore whether women with first-born daughters have greater reproductive success, as found among Gypsies (Berezckei and Dunbar 2002). In other species labeled “cooperative breeders,” the helpers either reproduce very little or not at all, spending their time helping one breeding female. We will explore the extent to which cooperative care affects the timing of reproduction in Hadza females.

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Appendix

In addition to analyzing proportions (percent of scans in which people were holding), we also analyzed counts of holding using non-parametric tests in which instances of holding were weighted by number of observations, giving greater weight to those individuals who appeared in more scans. Because we used counts of observations and included every instance of holding, our sample sizes were larger than the sample sizes used in the proportional data analysis. Nearly all of the results were replicated using the non-parametric analyses. The only result that differed was the amount of time female and male allomothers spent holding children. Using counts of holding, female allomothers spent significantly more time holding children than male allomothers (Wilcoxon rank sum $W=1,952$, $p=0.02$). The difference in results may be explained by the difference in sample sizes.

All of the following tests yielded the same results as when proportional data were used. The sex of a child was not associated with the amount of time a child was held (Wilcoxon rank sum $W=808$, $p=0.90$) and younger children were held significantly more often than older children ($R^2=0.55$, $p<0.0005$; the dependent variable is the log frequency of being held). Children were held by related allomothers significantly more often than by unrelated allomothers (Wilcoxon sign rank $V=1,089$, $p=0.02$, $n_1=42$ related, $n_2=39$ unrelated; from the point of view of the child) and more frequently by maternal relatives than paternal relatives (Wilcoxon sign rank $V=386$, $p<0.05$, $n=75$ children <4 years). When controlling for residency in camp, maternal grandmothers did not hold significantly more than paternal grandmothers (Wilcoxon rank sum $W=165$, $p=0.64$). For the child, the presence of maternal grandmothers and fathers in camp was not independent (Pearson's $\chi^2_{1, 75}=13.07$, $p<0.05$).

Two separate analyses were performed in order to determine whether holding was a product of kin selection. First, we used pooled proportions (all counts of allomaternal holding; mother excluded) to perform a logistic fit over the three levels of relatedness (0.5, 0.25, and 0.125 as predictors). Under the assumption of logistic relationship, degree of relatedness is a significant predictor ($p<0.0005$) of holding. The second analysis is a difference-of-proportions test involving two separate comparisons across the three levels of degree of relatedness. Individuals who are 0.5 degrees of relatedness are holding significantly more than individuals who are 0.25 degrees of relatedness ($\chi^2=6.65$, $p<0.0005$). Individuals who are 0.25 degrees of relatedness are holding more than individuals who are 0.125 degrees of relatedness ($\chi^2=94.21$, $p<0.0005$). In order to control for age of the child, we used regression to determine if the inclusion of age was lessening the effect that the degree of relatedness had on the frequency of being held. In both cases it did not.

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