Cooperative reproduction in Ituri Forest hunter-gatherers: Who cares for Efe Infants?

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Efe foragers of the Ituri Forest, Democratic Republic of the Congo, share in a unique child-rearing system in which infants receive care from many individuals other than their mothers from birth into early childhood (Tronick, Morelli, and Winn 1987; Tronick, Morelli, and Ivey 1992). Cooperative reproduction is highly unusual from an interspecific perspective and is especially challenging to evolutionary theory, compelling primatologists and biologists to devote considerable attention to parenting behaviors exhibited by alloparents (individuals other than the parent) toward conspecific young (e.g., Reimann 1982, Emlen 1984, McKenna 1987, Small 1990, Clutton-Brock 1991). From an explosion of research on animal behavior since the 1960s, three general hypotheses have come to dominate ecological perspectives on apparently altruistic parenting behaviors: nepotism, reciprocity, and learning-to-mother.

1. Nepotism predicts a substantial amount of variation in alloparenting both within and between species (McKenna 1987). Investing in kin is considered an extension of investing in one’s own genetic reproduction, as the degree to which genes are shared is expected to predict shared fitness interests. This equation, however, like all evolutionary predictions, is economic in nature and weighted by the relative costs and benefits to individuals of alternative behaviors within a specific environmental context (Williams 1966, Altmann 1979, Emlen 1995). The costs and benefits of particular behavioral strategies are determined by ecological interactions of the social and physical environment and individual life-history parameters affecting survival, growth, development, and reproduction. Human life history sets the stage for at least two important opportunities for kin, as well as others, to care, with important coevolutionary consequences. Parents nurture multiple weaned dependents,

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increasing the demand for and availability of care [Lancaster 1997]. Consistent with theoretical indications that a lengthy developmental period favors allocate by retained related "helpers-at-the-nest" [Lack 1966, Brown 1987, Koenig et al. 1992], sibling care is the most common form of alloparenting in traditional societies [Weisser and Gallimore 1977]. In addition to the prereproductive period, early female reproductive senescence may increase the probability of completing investment in later-born young [Lancaster and King 1985, Hill and Hurtado 1991, Hawkes et al. 1998] and enhance the reproductive efforts of adult offspring through assistance in food gathering [Hawkes 1997] or child care [Hill and Hurtado 1996].

2. Reciprocity. Other interspecific research suggests that where the costs of aiding unrelated young are less than the costs of leaving the group (e.g., because of predation pressure, low food availability, or social competition), unrelated helpers may assist parents in return for enhanced access to physical (e.g., food, territory) and social (e.g., alliance, mating) resources necessary for reproduction [Ligon 1983, Berrill 1984, Davies 1990]. Emi [1982a, b] modeled the fitness payoffs of helping between unrelated individuals, concluding that contributing resources to the reproductive success of an unrelated individual would be a successful strategy for both helper and beneficiary if they resided in a marginal environment with highly unpredictable access to the resources necessary for reproduction. Comparative analyses suggest that cooperative breeding is found in environments that are extremely limited in resources or saturated with conspecifics, limiting opportunities for juvenile or subordinate individuals to secure food, mates, space, or other resources necessary for individual survival [Clutton-Brock 1991]. By definition, small traditional societies lack the intensive stratification that results in large-scale subversion of the reproductive interests of some members of the group to the advantage of others. However, cross-cultural research confirms that demographic, economic, and social limitations commonly impinge on an individual's ability to mate and parent young in these populations [Irons 1983, Hill and Kaplan 1988a, b, Bailey 1991a, Hill and Hurtado 1996]. The extent of cooperative behavior exhibited within human groups, on a scale unparalleled in other species, suggests that in some ecological contexts allocate by unrelated but frequently interacting individuals may be included in the suite of shared and reciprocal social behaviors, such as cooperative resource acquisition and food sharing, that characterize traditional behavioral patterns.

3. Learning-to-mother. Like the reciprocity hypothesis, the learning-to-mother hypothesis predicts that personal but delayed fitness benefits are associated with alloparenting. Through skills gained from caring for the young of others, prereproductive individuals may increase the chances of survival for their own future offspring without incurring the risks to their young of inexperienced care [Spencer-Booth 1970, Lancaster 1971, McKenna 1987]. This hypothesis is based on several observations: (a) parenting skills do not appear to be innate among primates; (b) survivorship among primate offspring is highly dependent on the quality of care they receive; and (c) the infant mortality rate for primiparous female primates is higher than that for multiparous ones. Field studies report increasing reproductive success with age due to increasing reproductive skills in a number of nonprimate species as well [Lack 1966, Charlesworth 1980, Clutton-Brock 1988]. Perhaps in no species is the quality of care more critical to developmental outcome and future reproductive success of young than in humans, with important life-history consequences for parents, caregivers, and their wards [Boyn 1998, Charlesworth 1988, Hrdy 1992, Chisholm 1999]. As predicted by their future role as mothers, cross-culturally, young girls most frequently perform allocate [Barry, Bacon, and Child 1957, Weisser and Gallimore 1977].

The hypotheses of nepotism, reciprocity, and learning-to-mother suggest specific life-history strategies for alloparenting the young of others (table 1). Evolutionary ecological theory predicts that caregivers will allocate investment on the basis of the inclusive-fitness costs and benefits of providing care, with individuals giving care to the closest dependent who is likely to benefit from child care efforts. The probability and amount of investment should be determined by (1) the degree of relatedness between the potential caregiver and the child and (2) the ratio of the cost of care to the caregiver's fitness to the fitness benefit received by the child. While ecological theory implies an economic impact (i.e., cost or benefit) of behavior on individual reproduction, measuring the survival or reproductive consequences associated with specific behaviors remains challenging [Rogers 1990, Clutton-Brock 1991, Lessells 1991, Kaplan 1997]. The potential overlap of individual investment interests (e.g., kinship and reciprocal interests) and the competing tradeoffs of alternative behaviors (i.e., opportunity costs) complicates the task of assigning costs and benefits of behaviors to individual fitness. With regard to these constraints, this investigation assumes a temporally proximate focus: to examine the distribution of Efe infant allocate across caregivers to assess the explanatory strength of alternative hypotheses.

**Alloparenting among the Efe**

While some form of allocate has been described, at least qualitatively, in most hunter-gatherer societies, the most
extreme example of alloparenting in a foraging population has been reported for the Efe of the Ituri Forest. Data collected in 1982–83 showed that the percentage of time young infants spent in physical contact with individuals other than their mothers increased from 39% at 3 weeks to 60% at 18 weeks. During observations infants were cared for by an average of 14.2 different persons, with a range of 5 to 24 [Tromick, Morelli, and Winn 1987]. Tromick et al. hypothesized that this communal pattern of care was a cultural adaptation to the thermoregulatory challenges faced by Efe infants. Infants on average weigh 2.4 kg at birth, a weight considered “at risk” in the Western medical context [Tromick and Winn 1992]. Peacock (1983) and Hewlett [1991] have suggested that the unique pattern of Efe infant care may be explained by high rates of infertility among reproductive-age Efe women. Tromick, Morelli, and Winn (1989), however, found that the frequency of care by nulliparous adult females did not account for the extent of alloparenting. A number of studies describe Efe child care from a developmental point of view [Tromick, Winn, and Morelli 1987; Morelli and Tromick 1991; Morelli 1987, 1997; Tromick, Morelli, and Ivey 1992]; however, it remains unclear why so many individuals among the Efe forfeit their time and energy to provide care to the young of others. This investigation was prompted by the challenge of alloparenting behavior to ecological precepts: Who cares for Efe infants, and what are the costs and benefits to alloparents of child care services rendered?

THE STUDY POPULATION

A corpus of research provides details of the environment and lives of the Efe [cf. Morelli 1987, Peacock 1985, Ellision, Peacock, and Lager 1986, Tromick, Morelli, and Winn 1987, Wilkie 1988, Fisher and Strickland 1989, Jenike 1987, Bailey and DeVore 1989, Bailey 1991a, Wilkie and Curran 1993]. The Efe are widely accepted to be the most traditional population of pygmies in Africa. They associate with horticultural groups in an elaborate exchange system whereby farmers trade cultivated foods and material goods [e.g., cloth and metal] for the valuable forest resources of meat, honey, medicines, and building materials [Wilkie 1989, Bailey 1991a]. The Efe periodically provide labor in the gardens of the Sudanic-speaking Lese; however, since the end of colonial harvest quotas in the 1960s, the severe deterioration of roads, and the collapse of the cash market since the 1980s, most Lese gardens have contracted to subsistence level. Labor demands are intermittent, and many Efe lack access to opportunities for garden work. While some Efe have established their own gardens, they tend to be small and communal, with low and unpredictable yields [Wilkie and Curran 1993]. Only one focal family in this investigation planted a small shared seasonal garden of cassava.

The Efe live in camps ranging from 6 to 45 people, with an average of 21. Typically, they clear a small area of forest (10–15 m diameter) and construct low huts in an open semicircle around a communal space in which most daily camp activities occur. Although descent is patrilineal and residence is viriloclal, maternal relatives may also live in the natal camp because of sororal marriage exchange between clans. Nuclear families share a hut, which is primarily used for storage and sleeping, and a cooking hearth, but children, including infants, are by no means restricted from playing, exploring, and even sleeping in other areas of camp. Efe women usually travel together in small groups to gather forest produce, such as fruits, nuts, tubers, and mushrooms, fish in the streams that traverse the forest, or forage for bananas, cassava, and sweet potato in abandoned gardens. Garden labor is highly seasonal; during planting and harvest Efe women may assist Lese women, and Efe men are usually engaged in horticultural work only to fell trees when new gardens are cleared from the forest. Efe males hunt with bow and arrow in groups, using dogs and hunters to flush game to waiting bowmen, or hunt primates solitarily by stealth. Camps move on an average of every six weeks in response to changing access to forest and horticultural resources, from near-village gardens during planting and harvest to deeper in the forest during prime honey, fishing, and hunting seasons [Bailey and Peacock 1988, Wilkie and Curran 1993].

METHODS

Data were collected between January 1988 and October 1989 in 18 camps within a 36-km radius of the Ituri Project research station in northeastern Democratic Republic of the Congo. The focal subject sampling technique [Altmann 1974, Borgerhoff Mulder and Caro 1985] was adapted to record the behaviors of infant and mother simultaneously across all contexts, with the infant as the priority focal subject. The focal sample consisted of 20 infants [13 females and 7 males] between 12 and 15 months of age. Infants were observed for eight 15-minute sessions sampled across two consecutive and typical days, evenly distributed across daylight hours. Behaviors were continuously recorded as they occurred on a laptop computer that simultaneously tracked real time, facilitating a calculation of the absolute duration of events. Time measures were adjusted to a 12-hour day. Scans recording the identity of all individuals within visual or close hearing range of the infant [i.e., within a reasonable distance to respond to infant distress] were conducted immediately before and after each block of continuous behavioral coding, and departures and approaches of individuals were recorded as they occurred, to calculate the total proportion of time that individuals were in physical proximity to the infant. All exchanges of material goods, including food and other resources, between parents and individuals other than dependent children were recorded, whether they occurred within coding periods or not. Systematic and informal interviews were conducted with mothers and other caregivers in an attempt to elucidate other avenues of reciprocity, including friendships and economic associations. The habituation period included several months of frequent and extended visits to camps. Because data were simulta-
necessarily collected for a longitudinal study of infant socioemotional development [Tronick, Morelli, and Ivey 1992], the observer was often known to the infant from birth or shortly thereafter. Interobserver reliability was established in the field with a colleague and calculated [Cohen’s kappa], yielding a mean kappa coefficient of .90 [range .85–.96] across all behaviors.

Demographic records for 8 of the 18 camps have been maintained since 1979 by Ituri Project researchers and local assistants. New records were created to include camps not included in prior censuses and were cross-verified in interviews with group members and members of associated camps and through independent data collected by a local assistant. The ages of many individuals in the study area were known from previous records and local census taking. Unknown ages were interpolated relative to known-age individuals and specific local historical events of known date and cross-checked with dental exams [for children] and interviews. Lineage histories of two or more generations’ depth have also been maintained by the Ituri Project researchers. Kinship was independently verified by Efe camp members and local assistants, and new records were created for the remaining camps. The Efe maintain distinctions between consanguineal, affinal, and fictive kinship, facilitating the calculation of genetic distance between infants and others.

Individuals identified as consanguinely related to the focal infant are ranked according to estimated genetic distance (e.g., full siblings are related .50 to an infant, aunts .25). Relatives related more distantly than an estimated .125 to the infant are grouped in the analyses. Individuals identified as not consanguinely related to the infant are treated as unrelated. An allocaregiver was defined as anyone other than the mother in physical or social contact with the focal infant.

The question “Who cares for infants?” may be conceptualized analytically in a number of ways. The logistic regression technique [Hosmer and Lemeshow 1989] is intuitively and theoretically appealing, as odds ratios assigned to categorical covariates in a model allow for a biologically meaningful interpretation (see Hill and Hurtado 1996). Because the probabilistic outcome variable is dichotomous (that is, allocare or not), other multivariate techniques are used to take advantage of the sensitivity and precision of the data set, where behaviors are measured continuously. The analyses include (1) general descriptive statistics of care across infants, (2) logistic regression modeling of the probability of allocare among potential caregivers, (3) linear regression modeling of demographic variables on time in allocare, (4) linear regression fit of allocarerecruiting time to classes of potential caregivers [e.g., boys, girls, adult males and females, postreproductive adults], (5) assessment of the cost of care to actual allocaregivers, and (6) analyses of ecological correlates of allocare. Data were recorded on a program designed by David Wilkie and analyzed in StatView 1998 and SAS statistical programs.

RESULTS

General descriptors. Across the 20 infants in the sample, the total population of potential allocaregivers, that is, anyone other than the mother in proximity to a focal infant during observations, is 412. Efe one-year-olds are in close proximity to a caregiver 100% of observed time and spend an average of 85% of observed time in direct care [i.e., physical contact or social interaction with a
Infants receive 41% of care from individuals other than the mother, and fathers present [two died before the infant was one year of age and two were absent from camp on extended hunting trips] averaged 8% of total care and 20% of alloparental care. The mean number of allocaregivers interacting with the focal infant during observations is 11, with a range from 2 to 21. Infant sex is not associated with the number or any demographic characteristic of caregivers or with the amount of care received.

Logistic regression model of the occurrence of allocare. Neither the proportion of time in proximity to an infant nor the sex of the potential caregiver is significantly associated with the probability of performing allocare. Age, however, is negatively related to the probability of care (univariate beta coefficient = .023, chi-square = 15.964, p < .0001). Table 2 presents the best-fit logistic regression model, controlling for proximity, sex, and age of potential interactant: reproductive status and genetic relatedness are significantly associated with the probability of allocare. There are no significant interaction effects between variables. Odds ratios presented assess how much a particular factor—controlling for others—increases or decreases the likelihood that alloparenting will occur, using the absent category [reproductively active [i.e., with dependent offspring] and unrelated [estimated genetic distance = .00]] as the basis of comparison. Preproductive individuals [4 to 17 years] are no more likely to perform allocare than reproductively active adults [18 to 49 years], but nonreproductive adults are 2.5 times more likely and postreproductive individuals [50 years and older] 3 times more likely to alloparent than reproductively active adults. The effect of relatedness is substantial: kin are more than twice as likely as nonkin to contribute to allocare, and siblings and fathers (genetic relatedness = .50) are over 17 times more likely to perform infant care.

Linear regression model of the amount of time spent in allocare. Variation in the amount of time that individual Efe devote to infant allocare is considerable, ranging from 0 to 5.8 hours per day. In a full model regression of independent variables describing the life-history variation of the 412 potential allocaregivers, time in proximity and the characteristics of sex, age, relatedness, and reproductive status strongly predict the amount of time that individuals spend caring for a focal infant as main effects (p = .0001) [table 3], accounting for 20% of the variance in time Efe engage in allocare of one-year-olds. There are no significant interaction effects. Relatedness accounts for only 3% of the variance in time in proximity to an infant and explains 16% of the variance in allocaregiving time. To standardize variance in access to a related infant between individuals within each group, z-scores of relatedness were assigned to potential allocaregivers, with similar highly significant results on allocaregiving time (p = .0001). The time spent in proximity to an infant is significantly related to the amount of observed time that individuals provide care in univariate analysis (p = .001) but explains little of the variance between individuals in allocaregiving time (r² = .03) and is controlled for in subsequent analyses.

Comparisons between individuals in allocaregiving time. The significance of relatedness to participation in alloparental care is apparent when more familiar and socially meaningful categories reflecting sex, age, and kinship are considered. Among females, sisters and aunts spend significantly more time interacting with infants than sex- and age-matched unrelated individuals (fig. 1). While the mean proportion of observed time in allocare is several times higher for grandmothers than for unrelated age-matched females [grandmothers = .09 n = 4], others = .02 n = 8], the sample sizes are small, limiting significance testing. It is of interest that while grand-
mothers perform more allocare than other older women, because of high mortality very few infants or their mothers have access to grandmaternal care. Among males, only fathers, brothers, and cousins spend more time in allocare than do sex- and age-matched unrelated Efe [fig. 2].

Overall, differences between the sexes in time allocation to alloparenting are significant, but the prediction of increased allocare by females over males does not hold across all ages [fig. 3]. When ages are grouped into 10-year intervals, the mean amount of time spent in interaction is actually greater for males than females in the youngest age-range, from 0 to 9 years, although the difference does not reach significance. There is no significant difference between the sexes until reproductive age at 20 to 29 years, when the mean for males declines sharply. When fathers are excluded from the analyses, there is a significant difference in allocaretaking time between males and females throughout the reproductive period (i.e., 20 to 49 years). Sex differences for postreproductive-age adults, 50 years and older, approach but do not reach significance (p = .08), with older females contributing more than males to infant care.

Reproductive status has an independent effect on the time that Efe women devote to infant allocare, controlling for the effects of age. Reproduction (i.e., parenting) influences the allocaregiving time of reproductive-age females but not reproductive-age males, whether measured as the presence or number of dependent offspring, the age of the youngest dependent, or the presence of a nursing infant. With the exception of fathers, reproductive-age males perform little allocare. While prereproductive and postreproductive females do not differ significantly from reproductive-age women with or without dependent offspring, nonreproductive women spent significantly more time in infant allocaregiving than reproductively active women [fig. 4]. There is a suggestion that nursing mothers are especially constrained (or uninterested) in alloparenting: the mean amount of allocare that nursing mothers perform is half of that of mothers without nursing infants.

Regression fit to hypothesized allocaregivers. Separate regressions were fit for categories of allocaregivers predicted by theory (table 4). Only relatedness to the infant weakly predicts alloparenting by adult males (18 years and older) excluding fathers, and no variables predict care by postreproductive (50 years and older) males. The time that prereproductive age males (4 to 17 years) spend interacting with an infant is positively associated with relatedness and negatively associated with the number of dependents (i.e., siblings and foster children) in their own families. If siblings of the focal infant are removed from the analysis, the number of dependents in the family is no longer significant, suggesting that males provide care to infants when there are few other dependents to assist parents. Similarly, allocaregiving by young females (4 to 17 years) is predicted by relatedness and the presence of siblings in their own families. Again, only care by sibling allocaregivers is significantly affected by other dependents in the family. Relatedness alone is predictive of allocaregiving by nonsibling children. Only time in proximity to an infant is related to care by reproductive-age women (18 to 49 years) without dependent young, and only relatedness is predictive of allocaregiving by women with dependent offspring. Time spent alloparenting by postreproductive-age (50 years and older) women is predicted by relatedness alone.

Reciprocity and resource exchange. Resource exchanges involving fathers proved impractical to track outside the camp context, and there is no relation between paternal exchanges in the camp setting and allocaregiver participation. Hunted resources are primarily distributed at the kill site, and secondary distributions of meat often occur outside the camp context (e.g., in trade with horticulturalists). Occurrences of resource exchange involving mothers outside of the nuclear
TABLE 4
Regression Models of Observed Time in Allocaregiving Fit for Hypothesized Categories of Allocaregivers

<table>
<thead>
<tr>
<th>Category and Variable</th>
<th>Coefficient</th>
<th>p</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males excluding fathers</td>
<td>.005</td>
<td>.0564</td>
<td>.20</td>
</tr>
<tr>
<td>Relatedness</td>
<td>.127</td>
<td>.0002</td>
<td>.15</td>
</tr>
<tr>
<td>Prereproductive males (90)</td>
<td>.007</td>
<td>.0649</td>
<td></td>
</tr>
<tr>
<td>Relatedness</td>
<td>-1.9</td>
<td>.0270</td>
<td></td>
</tr>
<tr>
<td>Prereproductive females (70)</td>
<td>.533</td>
<td>.0024</td>
<td>.28</td>
</tr>
<tr>
<td>Relatedness</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Presence of siblings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nonreproductive females (33)</td>
<td>.600</td>
<td>.095</td>
<td>.20</td>
</tr>
<tr>
<td>Time in proximity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductively active females</td>
<td>.160</td>
<td>.0584</td>
<td>.09</td>
</tr>
<tr>
<td>Relatedness</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Postreproductive females (23)</td>
<td>.326</td>
<td>.033</td>
<td>.20</td>
</tr>
</tbody>
</table>

household are surprisingly infrequent, and there is no association between individuals who receive food or other resources (including child care) from mothers and the relatedness or allocaregiving contribution of the recipient. Women typically forage together in small groups, but with the exception of fishing and occasional abundant food patches resources are usually collected individually and, in the case of food, distributed after processing to children and other dependents in the household. The Efe possess few material resources, such as clothing or tools, and the transfer of these goods also does not appear to be associated with allocare.

There is also no relation between women identified by mothers as “friends” (described as individuals that mothers tend to associate and share with most frequently or those who might provide care for the mother or her family in case she were ill) and resource exchanges, relatedness, or allocaregiving. It may be of interest that 60% of women identified as “friends” [n = 25] have no dependent offspring and that, while nonreproductive women represent 32% of the total population of reproductive-age [18 to 49 years] women, they account for only 12% of alloprentral care received by infants. Women with children closely associate with one another but do not habitually share child care responsibilities. Efe alloprentrtning is not characterized as a creche or nursery system whereby mothers leave their infants in camp with others for extended periods while foraging: 92% of observed time mothers were within visual or close hearing range of their infants. Instead, working mothers are often accompanied by other, less burdened helpers, such as children.

The presence of foster children among the Efe suggests that alloprentrtning by some juveniles may be reciprocated with provisioning and protection by adults. Indeed, 27% of children have no parents in camp—orphans, children of separated parents, or those living temporarily away from natal camps—and Efe children are commonly transferred from high-dependency-ratio families to low-dependency-ratio families for a period of months or even years. While children 4 to 17 years of age without parents living in the camp do not contribute significantly more time in allocaregiving than children with parents residing in camp (excluding siblings of the infant in the comparison), foster children residing in a subject infant’s nuclear family [n = 11] spend significantly more time providing allocare than do other nonsibling children in the camp (Mann-Whitney U, p = .0035). This finding holds when relatedness to the infant is controlled for in the analysis. Foster children are related on average .10 to focal infants. In fact, the mean amount of allocare that foster children in the subject family provide exceeds that of siblings, although the difference does not reach significance. The Efe commonly recruit older children, both male and female, who are orphaned or belong to large sibships to assist primiparous mothers or mothers who lack older offspring to assist with infant care. However, not all new mothers have access to the services of

TABLE 5
Distribution per 12-Hour Day of Mean Time in Care of Focal Infant, Active Care, and Simultaneous Economic Activities by Actual Caregivers [n = 222]

<table>
<thead>
<tr>
<th>Caregiver*</th>
<th>n</th>
<th>Mean Time (hr.min)</th>
<th>Active Care (hr.min)</th>
<th>Economic (hr.min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mother</td>
<td>20</td>
<td>6:01</td>
<td>1:16</td>
<td>1:23</td>
</tr>
<tr>
<td>Father</td>
<td>14</td>
<td>0:50</td>
<td>0:08</td>
<td>0:07</td>
</tr>
<tr>
<td>Sister</td>
<td>15</td>
<td>1:08</td>
<td>0:11</td>
<td>0:05</td>
</tr>
<tr>
<td>Brother</td>
<td>26</td>
<td>0:47</td>
<td>0:06</td>
<td>0:03</td>
</tr>
<tr>
<td>Aunt</td>
<td>6</td>
<td>1:16</td>
<td>0:12</td>
<td>0:07</td>
</tr>
<tr>
<td>Uncle</td>
<td>3</td>
<td>0:28</td>
<td>0:02</td>
<td>0:00</td>
</tr>
<tr>
<td>Grandmother</td>
<td>3</td>
<td>1:35</td>
<td>0:08</td>
<td>0:18</td>
</tr>
<tr>
<td>Grandfather</td>
<td>1</td>
<td>0:33</td>
<td>0:00</td>
<td>0:00</td>
</tr>
<tr>
<td>Related female child</td>
<td>7</td>
<td>0:32</td>
<td>0:02</td>
<td>0:05</td>
</tr>
<tr>
<td>Related male child</td>
<td>10</td>
<td>1:02</td>
<td>0:14</td>
<td>0:05</td>
</tr>
<tr>
<td>Related female adult</td>
<td>1</td>
<td>1:42</td>
<td>0:00</td>
<td>0:00</td>
</tr>
<tr>
<td>Related male adult</td>
<td>0</td>
<td>0:00</td>
<td>0:00</td>
<td>0:00</td>
</tr>
<tr>
<td>Unrelated female child</td>
<td>29</td>
<td>0:16</td>
<td>0:04</td>
<td>0:01</td>
</tr>
<tr>
<td>Unrelated male child</td>
<td>30</td>
<td>0:09</td>
<td>0:02</td>
<td>0:01</td>
</tr>
<tr>
<td>Unrelated female adult</td>
<td>38</td>
<td>0:37</td>
<td>0:09</td>
<td>0:10</td>
</tr>
<tr>
<td>Unrelated male adult</td>
<td>19</td>
<td>0:11</td>
<td>0:02</td>
<td>0:03</td>
</tr>
</tbody>
</table>

*Categories are mutually exclusive. For example, related female child excludes sisters and related adult female excludes mothers, aunts and grandmothers, etc
*All fathers available [n = 16] were observed interacting with infants, but only 14 were engaged in allocare during focal data collection periods.
*Of the 10 related male children in the sample who care for focal infants, 7 were foster children. One related female child of 7 was a foster child. Two of the 30 unrelated male child caregivers and none of the 29 unrelated female child caregivers were foster children.

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other children. Six of the 20 subject infants do not have older siblings and 9 have no siblings older than five years of age, but only 3 of these have a foster child living in the nuclear family. Foster children tend to live in families with other children and are therefore subject to increased competition over familial resources. Direct assistance in infant care may be one means by which foster children can reduce conflict over scarce food resources within their adopted [i.e., alloparental] family. Efe children, and especially siblings, at times do receive directives from mothers to watch an infant, but the distribution or frequency of maternal directives does not predict children’s contributions to allocate.

The costs of alloparenting. If alloparenting is a costly activity in terms of time, energy, or lost opportunity, we would expect obvious benefits to be accrued by participants; however, no directly measurable reciprocal payoffs are found between parents and helpers. There are no data on allocaregiver time allocation independent of care to assess the impact of infant interactions on alternative activities; however, the average total time per day spent in allocaregiving and the nature of that care suggest a pattern of potential costs. Table 5 shows the distribution of time spent caring for an infant across categories of actual [as opposed to potential] caregivers [n = 222]. Maternal infant care time well surpasses that of allocaregivers, but the investment of some alternative caregivers is not negligible. Mothers spend an average of six hours a day caring for their infants, but the cumulative addition of a number of related caregivers results in substantial allocare. Of those who provide care, related children [4 to 17 years of age] and adults [18 years and older], including fathers, spend around an hour a day providing infant care. Unrelated caregivers, especially males, spend much less. Unrelated adult female allocaregivers, however, spend on average 37 minutes a day engaged in allocare, and there is no significant difference between the time contributions of unrelated nonreproductive and reproductive caregivers. Figure 5 illustrates the distribution of allocare across actual caregivers from the infant’s perspective. Perhaps most notable, males, including fathers [11%], provide an average of 46% of allocare received by infants, and unrelated adult females contribute nearly 20%. Children account for 56% of allocare. While the time contribution per caregiver often may be low, the cumulative time in allocare received by Efe infants is remarkably high.

Time is a global measure of investment; however, the multifaceted demands of infant care present varying costs to the caregiver. A second measure of the cost of care can be inferred from the nature of caregiving. Many forms of child care preclude or circumscribe participation by the caregiver in other activities, such as maintenance and economic tasks, travel, and attention to other children. Active care behaviors, such as feeding, grooming, bathing, carrying, and comforting a fussing baby, enlist a caregiver’s attention and participation to a greater degree than do physical contact [i.e., touching or holding] and social interaction [e.g., playing with and talking to an infant] alone. Table 5 shows that while mothers on average spend over an hour per day feeding, grooming, bathing, carrying, and comforting their infants, allocaregivers spend little time engaged in intensive infant care tasks.

A final approach to the assessment of the potential costs of allocare is the proportion of caregiver interactions that are performed simultaneously with economic tasks. While 23% of maternal infant care time is spent in simultaneous economic tasks, including household maintenance activities, manufacturing, water and firewood collection, food acquisition, and food processing [totaling over an hour of maternal time co-occurring with direct infant care], other allocaregivers spend very little time simultaneously negotiating infant allocare with economic demands [table 5]. Mothers are the most pressed for time to complete economic tasks [Peacock 1985], and the time and opportunity costs of allocare for other Efe appear to be low. Efe infant-allocaregiver interactions are characterized primarily by intermittent play and physical contact rather than more demanding forms of care and are relatively free from the burden of simultaneous economic tasks.

Ecological correlates. The diverse physical and social contexts of Efe life present opportunities and constraints that may be expected to facilitate or limit alloparenting. There is remarkable consistency, however, in Efe allocare across demographic and physical settings. Group size—the number of camp members present during observation—approaches significance in predicting the number of caregivers that infants experience [p = .07] but does not predict the amount of allocare they receive. There is no relation between allocaregiving time and season of observation [wet versus dry or clearing and planting versus peanut harvest, honey, or rainy], camp location [near horticultural villages versus an hour or more’s walk into the forest], or the demographic composition of
camps [e.g., number of individuals related to the infant, proportion of children to adults, number of nonreproductive adult females, number of foster children].

A clue to the remarkable consistency of Efe allocaregiving across physical settings may lie in Efe social ecology, where an apparent fluidity of social resources exists such that allocaregivers may be recruited or volunteer in the absence of others. As reported above, care by both male and female siblings is negatively associated with the presence of other dependents in the family. Surprisingly, there is no difference in the amount of allocare received by infants with and without siblings [no sibs n = 6, mean = 46%, with sibs n = 14, mean = 39%]. Paternal infant care is predicted only by siblings in the family older than five years of age [Mann-Whitney U, p < .05], whose presence is negatively related to the amount of time fathers give care, and an absence of siblings in the infant's family is associated with care by nonreproductive women [chi-square 4.615, p = .0317]. It appears that when parents lack kin to help, unrelated caregivers are recruited. The number of unrelated allocaregivers is negatively associated with the number of relatives available [i.e., in proximity] to an infant [p < .05, r² = .30]. Such assistance makes a difference to mothers: Mothers spend more time working when not engaged in infant care [p < .05], and nearly half of the variation in maternal care is explained by variation in the number of allocaregivers [p < .001, r² = .49] (Fig. 6).

There is some indication that alloparenting benefits Efe infants as well: the number of allocaregivers at one year of age is positively associated with survivorship at three years of age [survivors' n = 15] mean = 10.8 allocaregivers, nonsurvivors' n = 5] mean = 6.2 allocaregivers [Mann-Whitney U, p = .05; logistic regression log likelihood −8.410, chi-square 3.394, p = .0653, odds ratio = .664]. No other demographic or behavioral variable measured predicts infant survivorship.

**Conclusion**

The extensive social distribution of Efe infant care and the lack of impact of physical or demographic setting on the amount of allocare that infants receive suggests a highly flexible child-rearing system that recruits the diverse investment interests of relatives and nonreproductive individuals, especially adult females and children, facultatively in a low-cost, potentially high-benefit endeavor. When the investigator queried a caregiver, "Who cares for Efe infants?" she responded matter-of-factly: "All of us." While this descriptor paints too communal a picture of Efe infant care (on average about one-third of camp members are related to the infant, about half provide infant care, and mothers remain responsible for the majority of direct care of one-year-olds), it does reflect a confluence of social interests in the care of young. These data are consistent with previous analyses of Efe care of young infants [e.g., Tronick, Morelli, and Winn 1987, Winn 1991] and older children [e.g., Morelli 1987, Tronick, Morelli, and Ivey 1992]. Efe child-rearing demonstrates the central role of human life history and social ecology in providing the opportunity for multiple modes of cooperation in parenting, including nepotism, reciprocity, and learning-to-mother. The suggested lack of significant costs of alloparenting among the Efe reduces the theoretical demand of finding its compensation, and mutualism, whereby individuals gain greater benefit by acting together than alone [see Wrangham 1982], may best characterize Efe allocare. With the exception of a number of reproductive-age females without young, the demographic profile of an Efe allocaregiver is much like what could be found in any small foraging group.
population: All human groups are composed of females, relatives, and nonreproductive members, including children and postreproductive adults, begging the question of the uniqueness of Efe allocate. Efe allocate is neither communalistic nor entirely nepotistic, and values concerning infants do little to explain the pattern of caregiving.

The life history and ecology of the Efe hold clues that productive as well as reproductive constraints facilitate allocate by affecting the access that individuals have to food and social resources. Time allocation data (Bailey and Peacock 1988, Peacock 1985, Ivey 1993) and local interviews (Ivey 1993) suggest that Efe mothers face considerable demands in provisioning their families. Because Efe children are nutritionally stressed (Bailey 1991b) but able to gather little in the way of food for themselves (Ivey, Morrelli, and Tronick 1994, Morrelli 1997), they may defray some of the costs of parental provisioning by performing tasks that increase adult economic efficiency (see Blurton Jones 1993). Mothers are relieved of competing child-care demands to engage in subsistence activities from which children and others benefit. In addition, high rates of mortality and infertility render access to kin low or unpredictable for many Efe, but the reliance on social relationships for success in economic and reproductive activities is high (Bailey 1991a). The development of diverse social ties through allocaregiving may enhance the probability of future cooperation (Morelli and Tronick 1994, Ivey 1993), which has especially important long-term benefits in an environment of unpredictable (i.e., high-variance) access to resources (Low 1988). The role of child-care aid in cooperative reproduction remains underexamined, and these data suggest that among some foragers low-cost assistance may moderate the quality–quantity tradeoff of parental investment. Alloparenting therefore has important developmental and reproductive consequences with implications for the evolution of human life history.

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The proposition of Lewis-Williams and Dowson [1988, 1993] that many of the abstract marks found in Palaeolithic and Neolithic art can be put down to neurophysiological processes, as determined by shamanistic prac-

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