

Sexual selection and paternal investment among Aka pygmies

Introduction

Chagnon's extensive demographic work among the Yanomamö (1975, 1979a, 1979b, 1980, 1981, 1982) provided much of the early empirical field evidence to demonstrate that Darwinian hypotheses were useful in explaining some human behaviors. The few other field studies of evolutionary biology among humans came from populations similar to the Yanomamö where polygyny and accumulation of material resources existed (Gray 1985). Evolutionary predictions proposed by Darwin (1871) and Trivers (1972) (i.e. male-male competition for women) may appear to be more applicable in farming populations such as these where ritual warfare or competition for

land or prestige goods are central to the cultural system. Evolutionary theory has seldom been utilized for predicting human behaviors among hunter-gatherer populations which are often characterized as peaceful or egalitarian, and where monogamy and lack of property accumulation are more common (see Hill and Kaplan, this volume (Chapters 17 and 18) for an exception). This chapter examines the applicability of evolutionary theory among a foraging population that is better known for its peacefulness rather than its fierceness – the net-hunting Aka pygmies of the Central African Republic (see Figure 16.1).

¹ Department of Sociology and Anthropology, Southern Oregon State College, Ashland, OR 97520, USA

Quantitative evidence for sexual selection among Aka pygmies is sought by re-examining published and unpublished demographic data (e.g. Hewlett *et al.* 1982, 1986a, 1986b) collected between 1974 and 1984. Once the data pertinent to sexual selection has been examined, the relationship between sexual selection and Aka paternal behaviors is considered. That is, if sexual selection is occurring, does it help us to understand the Aka paternal behaviors? Again, existing data (Hewlett, 1986) on Aka fathers are re-considered from an evolutionary perspective. The re-evaluation of the Aka data in light of evolutionary biology ends up expanding our understanding of a number of Aka behaviors, but also indicates some limitations to this theoretical perspective.

Theory

Darwin was the first to emphasize the concept of sexual selection. He pointed out that individuals who do not differ in their ability to survive may differ greatly in their mating success (sexual selection). According to Darwin, sexual selection could occur in two ways: competition within one sex for access to members of the opposite sex, called intrasexual competition by Huxley (1938), or choice by individuals of one sex for a particular member of the opposite sex, which Huxley called epigamic selection. Darwin realized that in nature it was usually males who competed with each other for access to females,

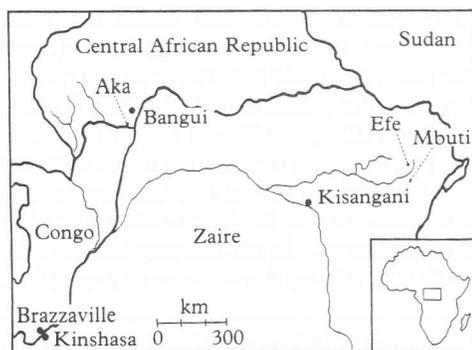
and that it was generally the females who selected particular males. The male-male competition he suggested could result in more extensive selection in males, that is, in greater variation in male reproductive success than in female reproductive success. Sexual selection is how Darwin accounted for traits that seemed unrelated to the struggle for existence (e.g. male antlers, tusks, fangs and bright plumage). But Darwin did not know why it was usually the males of most animal species which engaged in intrasexual competition and the females who did the choosing.

A. J. Batemans' (1948) experiments with *Drosophila melanogaster* provided some answers to Darwin's question. He quantitatively demonstrated that: (1) male flies had greater variation in reproductive success than did females, and (2) the frequency of copulation had no effect on female reproductive success (after the first copulation), but the more copulations a male had, the higher was his reproductive success. Bateman explained his results by suggesting that the male flies had more to gain by multiple, rather indiscriminate matings, while females did not. Females produced few and relatively costly eggs whereas males produced many and relatively inexpensive sperm. Since a male has more opportunity to increase his reproductive success by mating with many females, he may be willing to engage in intrasexual competition to gain access to females.

Darwin and Bateman's findings should be applicable to human populations (see, too, Trivers 1972). As with *Drosophila*, human males should benefit more from multiple matings than females. Human adult males invest less in reproduction than do females. Since there is a higher cost to female reproduction, females are predicted to invest more in infant care than are males. Holocultural studies have also shown that males are more likely to be the polygamous sex (van den Berghe 1979, Betzig 1986). According to Darwin and Bateman, these conditions predict greater intrasexual competition among males than among females.

Human males are expected to have greater intrasexual competition than females because males benefit more reproductively by multiple matings. The first section of this chapter examines three measurable consequences of male intrasexual competition, all of them taken from

Figure 16.1 Location of African pygmy groups mentioned in text.



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Trivers' (1972) discussion of sexual selection. First, if size of home range functions to increase matings, then one would expect larger home ranges among the more potentially polygamous sex (i.e. males). In ecological settings where females are a dispersed resource, males are predicted to have a larger home range than females because male mobility may be crucial in exposing the male to available females. Second, as a consequence of greater intrasexual competition among men, one would expect male mortality to be higher than female mortality, especially when reproductive potential is highest. Third, as a result of their higher polygamous potential, one would expect reproductive variance to be greater among men than among women.

The second section of the study considers the impact of sexual selection on human paternal investment patterns. From a cross-species perspective, human males are known for their investing – humans are one of the very few mammalian species in which males invest substantially in their offspring – while from a cross-cultural perspective, fathers are known for their lack of parental care. Cross-cultural studies have demonstrated that fathers invest very little time in the direct care of children in comparison to mothers (Whiting and Whiting 1975, Babchuck *et al.* 1985). Father's role also seems to vary considerably more cross-culturally than does mother's role (Barry and Paxson 1971, Katz and Konner 1981); there are the active indulgent !Kung fathers, for instance, and the Rwala Bedowin fathers who are separated from their children until they reach 7 years of age. Mother's role cross-culturally is less variable; Katz and Konner's holocultural study (1981) found mothers to be the primary caretakers in 90% of the societies investigated. Some mothers may be indulgent in their care and others perfunctory, but they are consistently active in caregiving.

Sexual selection could affect variability in paternal investment patterns within and between cultures. Parental effort can include time and/or resources. A way men might compete for matings is by accrual or expenditure of parental resources. Some men may successfully spend time garnering resources to be used as parental investment; men who cannot may compensate for their lack of resources by spending time with their children. These predictions will be consi-

dered for explaining intracultural (the Aka) and intercultural variation in paternal investment.

The Aka

The Aka pygmies are foragers of the tropical forest regions of the southern Central African Republic and northern Congo-Brazzaville. Two groups of Aka pygmies are included in this study; about 250 Aka associated with the village of Ndele and about 800 Aka associated with the village of Bagandu. Both villages are in the Central African Republic, Ndele being about 100 kilometres west and slightly south of Bagandu.

The Aka spend about 56% of their subsistence time in hunting, 27% of their time in gathering and 17% of their time in village work (Bahuchet 1987). Although the Aka net-hunt the majority of the year and spend little or no time in the cultivation of plant foods, they are transitional foragers in the sense that a large proportion of their diet comes from domesticated village products. Seldom does a day go by without Aka consuming some manioc. In the forest they trade game meat for manioc the farmers transport into the forest, and in the village they provide labor to their village trading partner for which they receive access to his fields. The Aka reside in the village three or four months a year, in part, to assist in the clearing of the villagers' fields.

As with the Mbuti pygmies of Zaïre (Turnbull 1965, Hart 1977), most camp members, males and females, young and old participate in the net-hunt. From the time Aka leave the village and return to the forest (February–March) until caterpillar season (July–August), they often net-hunt six days a week, four to nine hours per day. Net-hunts decrease in frequency during the caterpillar season (caterpillars provide about 40% of diet at this time of year) and the major rainy season (August–October); individual and small group foraging techniques (e.g. spears, crossbows, traps) are utilized more frequently during these seasons.

The Aka are patrilineal, having shallow patri-clans, and are usually patrilocal except for a few years after marriage when the male provides bride service in the camp of his wife's family. Aka kinship terms are basically generational; *tao*, for instance, refers not only to the natural father but to all of the father's brothers as well,

all grandparents are called *koko*, all offspring are called *mona* and brothers and sisters called *kadi*. As has been described for other hunting-gathering populations, the marriage and kinship rules are flexible and adaptive to situational constraints (Turnbull 1968, Woodburn 1968, Lee and Devore 1976, Chagnon, this volume (Chapter 1)).

There are four important demographic units: the nuclear family, the camp, the patriclan and the band. The camp (*lango*) consists of 1–15 nuclear families, but averages around 25–35 individuals. The core of the camp usually consists of adult males belonging to the same patriclan (*dibanda*); adult males not from the central patriclan are either temporary visitors or males providing bride service. The final demographic unit, the band, is a more elusive entity as the Aka do not have a native term for it. Essentially, it is a group of 60–100 individuals who hunt and gather in the same vicinity. Its core usually consists of two to four clans. During various seasons the band goes through periods of concentration and dispersal.

There are few Aka status positions. There is no chief in the sense of a person commanding ultimate authority, but there is the *kombeti*, who is generally an older adult male (but not aged) and who exercises his influence in subsistence and camp movement decisions in modest and subtle ways. The *nganga* is the traditional healer and provides a wide range of services to the community – e.g. divination on hunts, curing of witchcraft and herbal healing. The *ntuma* is the great elephant hunter who has often killed several elephants on his own. He leads important hunting and seasonal rituals and organizes the training of young boys in the men's secret society. If an *ntuma* exists within the camp he also often holds the position of *kombeti*.

Sharing, cooperation and autonomy are but a few of the core values of the Aka. Game captured on the net-hunt and manioc acquired through trade from farmers are shared among all camp members. Cooperation takes place each day on the net-hunt as well as in other subsistence activities. Autonomy is expressed daily as individuals in the camp decide to come and go as they wish.

Methods

The mortality data are based on interviews with 170 Aka adults from the Bagandu area and 147 Aka adults from the Ndele area (Hewlett *et al.* 1986b). Individuals were questioned about deceased parents, spouses and children, the illness that caused the death, approximate age at death and an estimated date of death. The fertility and marriage data come from 31 Aka adults over 41 years of age (13 males and 18 females) from the Ndele area and 30 Aka adults over 41 years of age (16 males, 14 females) from one section of Bagandu–Bokoka. These data come only from individuals that were known to me for some time and where cross-checking of birth histories with former spouses was possible. The data on exploration range and mating range are based on interviews with 42 adult males from the Bagandu area and 68 adult and adolescent males and females from the Ndele area (Hewlett *et al.* 1986a). The Bagandu Aka were questioned about visiting 43 places and the Ndele Aka were questioned about visiting 70 places.

Finally, the parenting data come from a sample of 15 Aka families with infants between 1 and 18 months of age associated with the Bokoka section of Bagandu (Hewlett 1986). Eight of the infants were female and 7 were male, 6 between 1 and 4 months of age (2 males, 4 females), 5 between 8 and 12 months of age (3 males and 2 females) and 4 between 13 and 18 months of age. Three types of focal sampling (Altmann 1974) were utilized: father focal all day (6 a.m. to 6 p.m.), infant focal all day and infant focal for 2 morning hours. While the infant or father was being followed some behaviors were measured continuously (e.g. holding, social interaction between caretaker and infant), while other behaviors were measured at 15-minute intervals (e.g. activity of infant/father, people touching infant/father, availability of father and mother).

Measurement of overall human parental investment is difficult. Non-human ethological studies have emphasized direct investment, such as holding, grooming, nursing and feeding of offspring. Little attention has been given to the more indirect forms of investing, such as proximity maintenance, status maintenance and inheritance of parents' resources. Although these forms of paternal investment will be considered in the analyses below, direct care will be

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emphasized because it was observable and, consequently, a relatively easy behavior to measure.

Results

Sexual selection among Aka

Figure 16.2 examines the fertility (number of live births) of 29 Aka men and 34 Aka women over 41 years of age. Although male variability is not as great as found in some polygynous Amazonian populations (Chagnon 1982, Daly and Wilson 1983:89), the predicted pattern of greater male variability is confirmed. For instance, male fertility ranged from no offspring to 14, whereas, female fertility ranged from 2 to 11 offspring. Aka male versus female variance fits well with the Aka pattern of 'limited polygyny' (about 15% of Aka males have more than one spouse); the variance is not as great as in more polygynous societies (Borgerhoff Mulder 1987), but is greater than in prescriptively monogamous societies (Brown and Hotra, this volume (Chapter 8)).

Aka males that are successful in intrasexual competition should have greater reproductive success. Aka leaders, such as the *kombeti*, could be considered successful competitors. One-third of the males in this position are polygynous while the average Aka polygyny rate is only 15%. Aka

Figure 16.2 Male and female reproductive success of Aka pygmies over the age of 41 years.

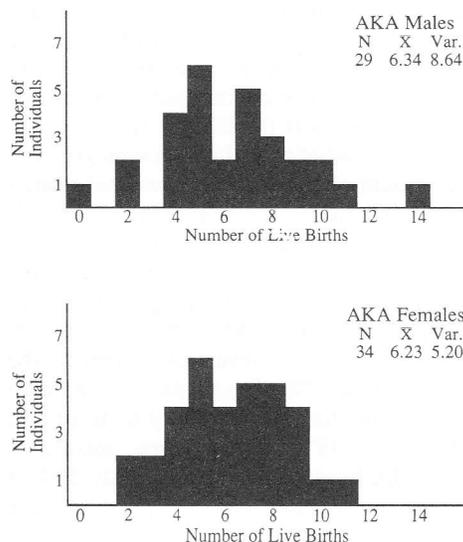


Table 16.1 Exploration ranges of Aka males and females

	n	M ^a	SD	SE	t	df
Males	18	60.7	33.8	8.2	2.2 ^b	17
Females	24	41.4	13.4	2.8		

^a Mean distance in kilometers

^b $p < 0.025$

males that hold the position of *kombeti* do experience greater fertility than males of comparable age, although the differences are not significant (9 *kombeti* over 41 years old sired on average 7.89 children while all males over 41 sired on average 6.34 children, $t = 1.30$, $df = 36$).

If range affects mating increases, then males should occupy larger ranges than females to ensure that they are exposed to a number of available females (Trivers 1972:165; Gaulin and Hoffman, this volume (Chapter 7)). Since Aka live in relatively small (25–35 individuals) scattered camps where population density is less than 0.5 persons/sq km, marriageable females are dispersed. Clan exogamy also implies individuals must go some distance to locate a marriage partner. Males have a significantly larger mean 'exploration range' (see Table 16.1) than do females. Males also exhibit a greater variance in exploration range than do females. This suggests that some males have to go farther than others to find a spouse, to trade or to work for a villager.

The same males and females were also asked about their birthplace. Calculation of distances between birthplace of spouses was then possible; this measure was called the 'mating range' (Hewlett *et al.* 1986a). For females there was no relationship between exploration range and mating range ($r = -0.022$), whereas for males there was a significant correlation ($r = 0.565$), thus indicating that Aka male exploration range was a function of the distance traveled to locate a spouse.

Darwin and Bateman also predict greater male mortality due to intrasexual competition. Based on a study of Aka causes of death, Figure 16.3 clearly demonstrates the predicted pattern – Aka males run a greater risk of mortality at every age. As in other human populations (Daly and Wilson 1983), adolescent and young adult males suffer the greatest relative mortality, largely as a result of greater risk taking (Wilson and Daly 1985). A total of 30% of the Aka male deaths

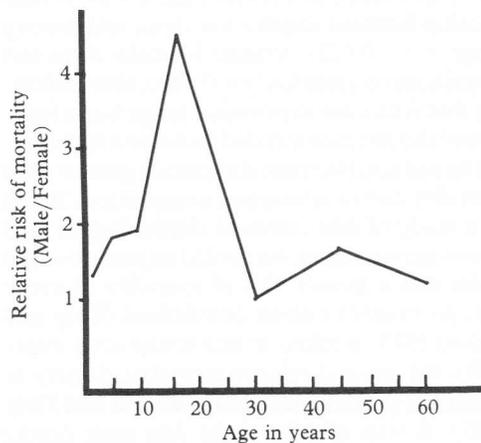
at this age were attributed to falling from a tree or some form of hunting and gathering accident.

In summary, Darwin's and Bateman's prediction that where one sex benefits more by multiple mating, one would expect more intrasexual competition, is supported by the Aka data: (1) Aka males ranged farther than Aka females; (2) Aka male mortality was greater than female mortality, especially in early adulthood; and, (3) Aka male reproductive variance was greater than female reproductive variance.

Aka paternal investment patterns

Aka fathers are exceptional in the fact that they provide more direct care (i.e. holding) to their infants than fathers in any other human society known to the literature (see Table 16.2 and Hames, this volume (Chapter 14)). Aka fathers are, on average, within an arm's reach or holding their infant 47% of the time in a 24-hour period. Infant holding demonstrates some of the distinctive qualities of father's versus mother's investment in young. First, fathers hold the infant less time overall, and when they do hold the infant, they hold it for a shorter period of time than the mother. Over a 12-hour period of observation during daylight hours, the father would on average hold his infant for a total of 57 minutes while the mother would hold the infant 490 minutes. The average duration of a father hold was 11.10 minutes, while an average mother hold lasted twice as long, 23.27 minutes. Second, the

Figure 16.3 Relative risk of mortality of Aka males and females.



context of mother and father holding was also markedly different. Table 16.3 shows that fathers held their infant primarily in the camp context when not engaged in an economic activity, while mothers held their infant frequently in either setting, but especially while engaged in economic activity (e.g. on the net-hunt). When a father does help out carrying the infant on the net-hunt, it is on the walk back to camp when the mother has a heavy basket of meat and nuts. Third, Figure 16.4 demonstrates some of the different activities of mothers and fathers while holding their infant. Mothers are more likely to be the providers of nourishment and the transporters of the infant while the fathers are more likely to hug and kiss or play with the infant as they are holding. Fathers invest in relatively brief and intense episodes of activity, such as play or affection, while mothers are more inclined to invest in longer more energetically demanding activities, such as transporting and nursing.

Maintenance of proximity to the infant can also be considered a form of parental investment. It could be essential in protecting the infant from environmental factors (e.g. predators, camp fires, other aggressive children), or in transmitting cultural knowledge, such as subsistence skills. It was not uncommon, for instance, to see parents transmitting subsistence skills (e.g. use of small digging stick, knife, spear) while sitting near their 12-month old infants. Table 16.4 demonstrates that while the father is frequently available to the infant in the forest setting, he is significantly less available than the mother. Table 16.4 gives mother and father availability while they are camped in the forest; when Aka camp near the village, this disparity in mother and father availability is even greater.

The amount of father holding was not related to father availability. While camped near the village fathers were much less available to their infants than while they were camped in the forest, but there were no significant differences in overall father holding between the forest and village setting. This is a result of fathers in the village spending 52% of their day in the camp when infant holding is most likely to occur and spending only 48% of their time outside of camp. In the forest, fathers spend only 29% of their time in the camp and 71% of their time outside of camp.

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Table 16.2 *Comparison of father holding in selected foraging populations*

Population	Age of infants (months)	Father holding (% of time)	Source
!Kung	0-6	1.9	West and Konner (1976)
	6-24	4.0	
Efe pygmies	1-4	4.0	Winn, pers. comm., 1985
Aka pygmies	1-4	22.0	This chapter
	8-18	14.0	

Note: All observations were made in a camp setting

Table 16.3 *Mean percent of time mother, father and others held focal infant during daylight hours in two forest contexts: in camp and on the net-hunt*

Age of infant (months)	Forest camp				Net-hunt			
	Mother	Father	Others	Total	Mother	Father	Others	Total
1-4 (n = 6)	51.0	22.0	27.8	100.0	87.3	6.5	6.2	100.0
8-12 (n = 5)	45.3	11.2	2.3	58.8	87.8	5.9	0.0	93.7
13-18 (n = 4)	31.8	14.3	9.4	55.5	88.9	2.4	1.1	92.4

Another form of parental investment is the training of offspring in skills essential to survival. A study of Aka cultural transmission (Hewlett and Cavalli-Sforza 1986) indicated that mothers and fathers contributed equally to the subsistence training of their children, but that fathers were more likely to educate sons and mothers more likely to educate daughters. Fathers were more likely to transmit hunting, dancing and singing skills while mothers were more likely to transmit gathering and childcare skills.

The intimate nature of father-infant interactions can also be demonstrated in the kinds of infant caretaking tasks fathers perform. Aka fathers sleep in the same bed as their infant, wife and other young children. When the child wakes up at night and is not comforted by nursing, it is the father who sings to the infant and, if necessary, gets up and dances with the infant until s/he stops fussing. While fathers hold the infant, they are likely to clean mucus from the nose, pick lice from the hair and pick dirt off the body. If the infant defecates or urinates, he

Figure 16.4 Parents' activities while holding infant.

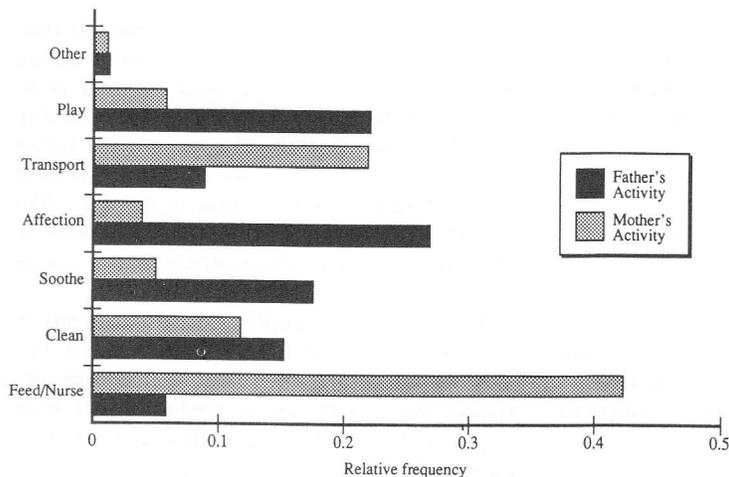


Table 16.4 Comparison of father and mother availability in forest setting

Parent	Within visual range					Within hearing range (but not within visual range)					Out of area				
	<i>n</i> ^a	<i>M</i> ^b	SD	SE	<i>t</i>	<i>n</i>	<i>M</i>	SD	SE	<i>t</i>	<i>n</i>	<i>M</i>	SD	SE	<i>t</i>
Mother	6	92.7	8.0	3.6	5.3 ^c	6	2.0	3.9	0.9	4.5 ^c	6	5.2	7.4	3.3	2.2 ^d
Father	15	63.6	15.2	4.1		15	21.9	7.2	1.9		15	14.5	10.4	2.8	

^a *n* = number of all-day observations

^b Mean scores are the average percentages of time fathers or mothers are available during daylight hours (6 a.m. to 6 p.m.)

^c *p* < 0.005 (df = 19) ^d *p* < 0.025 (df = 19)

Table 16.5 Mean numbers of minutes fathers held focal infant and some cultural and demographic variables

Min. held	Inf. age ^a	Number brothers	Number sisters	Living parents	Number wives	Status ^b father	Wife from trail ^c	Size ^d net
40.4	1	2	2	1	1	—	Yes	L
51.2	1	2	1	2	2	K	Yes	L
106.7	1	1	1	1	1	—	No	S
117.5	1	0	1	1	1	—	No	S
45.4	1	1	1	2	1	—	No	B
41.1	1	0.5	0.5	1	1	—	Yes	M
111.8	2	0	0	0	1	—	No	S
116.1	2	0	1	0	1	—	No	M
13.0	2	2	2.5	1	2	K	Yes	L
42.5	2	0	0	0	1	—	No	S
39.7	2	0.5	1	1	1	—	No	M
25.2	3	1	2	2	1	K	Yes	L
43.3	3	1	3	1	1	—	Yes	L
13.7	3	1	1	1	2	K	Yes	L
44.7	3	2	1	2	1	K	Yes	M

^a 1 = 1–4 months; 2 = 8–12 months; 3 = 13–18 months ^b K = *kombeti*

^c Yes = wife came from Aka clan that resides near same forest trail to village as husband; No = wife came from Aka clan that resides some distance from primary trail

^d S = small (less than 30 meters long); M = medium (31–60 meters long), L = large (greater than 60 meters long); B = bride service (no net of own being used)

cleans up the mess. If the infant wants to nurse and the mother is not around, he offers his own breast to the infant. When in the village camp, fathers carry their infants with them when they go drinking *mbolu*, palm wine, often giving some of the wine to their infants.

Aka intracultural variation in paternal investment

In comparing fathers who held their infant frequently with fathers who seldom hold their infant, a generalized pattern of traits emerged. High investment fathers tended to have the following traits: no brothers, few relatives in

general, wife from a distant clan, married relatively late in life, monogamous, a small hunting net, relied more on individual hunting techniques (e.g. small traps), had a close relationship with Ngandu villagers, and he and his father never held a position of status (i.e. never held the position of *kombeti*, *ntuma* or *nganga*). Aka fathers who seldom held their infant tended to have the opposite characteristics (see Table 16.5).

With the small sample size, it is difficult to determine which factor(s) is more important. Table 16.6 examines some factors that have previously been identified in predicting the level of paternal investment, and demonstrates that statistically significant differences are found

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Table 16.6 *Father holding and some demographic and life-cycle variables*

Variable	<i>n</i> ^a	<i>M</i> ^b	SD	SE	<i>t</i>
<i>Marriage type</i>					
Monogamy	12	68.4	36.0	10.8	
Polygyny	3	26.0	21.6	15.1	2.1 ^c
<i>No. of father's brothers</i>					
None	4	97.0	36.3	21.0	
Two	4	37.3	16.8	9.7	2.6 ^c
One (or half-brother)	7	44.7	29.5	13.2	0.4
<i>Infant birth order</i>					
First-born	7	71.1	40.2	16.6	
Later-born	8	44.1	30.6	11.5	1.3
<i>Household composition</i>					
Parents and infant only	7	73.4	37.4	15.8	
Parents, infant and sibling(s)	8	41.8	31.0	11.5	1.6
<i>Father's age</i>					
Under 30	7	72.0	39.2	16.1	
Over 30	8	43.2	30.4	11.5	1.4
<i>Sex of infant</i>					
Female	8	58.7	33.8	13.0	
Male	7	54.7	42.5	17.3	0.08
<i>Age of infant (months)</i>					
1-4	6	67.0	35.3	15.8	
8-12	5	64.8	46.1	23.0	0.08
12-18	4	31.7	15.1	8.6	1.3

^a *n* = number of fathers

^b Mean scores are the average number of minutes fathers spent holding their infant during daylight hours (6 a.m. to 6 p.m.)

^c *p* < 0.01

between fathers who have many brothers and those who have none, and fathers who are polygynous versus fathers that are monogamous. There is some indication that the number of brothers is slightly more important than polygyny. There is little difference, for instance, between the 2 monogamous fathers with 2 brothers and the 2 polygynous fathers with 2 brothers; the 2 brothers that are monogamous spent an average of 42 minutes holding their infants and the 2 brothers that are polygynous spent 38 minutes holding their infants. The number of brothers is important because the patrician forms the core of the hunting-collecting unit. If a male has a few brothers he is more likely than a male with no brothers to have a reliable economic unit. Females prefer to marry into a more economically reliable group so they seek males who have more brothers (cf.

Berté, this volume (Chapter 4)). Consequently, males with a few brothers do not have to travel as far to find a spouse and can marry earlier as more females are attracted to them. This in turn also means that the family of the wife is nearby to help support the family. Since the father who holds his infant frequently does not have a group of brothers to rely on for cooperation on the net-hunt, he relies more on individual or small-group hunting techniques and is more likely to provide labor to Ngandu farmers.

The data suggest that higher status fathers, that is those with more resources (brothers), invest less direct care in their infants. A high status male is one who has many brothers, two wives and has a father who was an *ntuma* or *kombeti*. Indirect evidence exists to suggest that fathers with more brothers are of higher status and have in fact more resources. First, of the 7 *kombeti* in the study areas for which reliable geneological data exist, all had at least two full brothers. Second, higher status Aka males (i.e. those in position of *kombeti*) had significantly fewer caries than males of the same age (Walker and Hewlett 1987), suggesting that they had a diet higher in protein and fat. The better diet may also explain why the *kombeti* are on average 3 cm taller than the average adult Aka (i.e. they have had better diets than other adult males). One might infer that their children may also have a better diet as a consequence of having a higher status father. Third, as demonstrated earlier, the *kombeti* generally has more than one wife and more children, a sign that he has more resources. Greater reproductive success of the *kombeti* would contribute to the future status and reproductive success of the child. This does not mean that the father who does not hold the infant contributes less; he provides different types of investment. For instance, much of his time may be spent talking with other males so as to maintain his status. This status maintenance 'indirectly' benefits the infant. Fathers with fewer resources (brothers) compensate by spending more time in the direct care of their infant.

Finally, cultural explanations for this variability should also be considered in future studies. The cultural transmission study mentioned above demonstrated that Aka culture is transmitted primarily from parent to child. According to a cultural transmission model developed by Cavalli-Sforza and Feldman (1981), this form of

Table 16.7 *Comparison of father presence with infants or children among selected foraging and farming populations*

Population	% of time father is present or within view during observations	Primary setting of observations	Source
Gusii	10	house/yard and garden	1
Mixteca	9	house/yard	1
Ilocano	14	house/yard	1
Okinawan	3	public places and house/yard	1
Rajput	3	house/yard	1
!Kung	30	camp	2
Aka pygmies	88	forest camp	3

Sources:

1. Whiting and Whiting 1975
2. West and Konner 1976
3. This chapter

transmission predicts great intracultural variability – precisely what we find in paternal investment patterns. Unfortunately, longitudinal data to test the model (i.e. to determine if investing fathers socially reproduce high investing fathers) do not exist.

Intercultural variation in paternal investment

Like many other foragers, the Aka have few accumulable resources that are essential for survival. Males essentially inherit a most important resource, brothers. Aka males also contribute slightly fewer calories to the diet than do females (considering that females also contribute on the net-hunt (Bahuchet 1987)). In societies unlike the Aka, where resources essential to survival can be accumulated or where males are the primary contributors to subsistence, sexual selection theory would predict that fathers in these societies would invest more time competing for these resources and consequently would spend less time with their children. In contrast, where resources are not accumulable or men are not the primary contributors to subsistence, men overall would spend more time in the direct care of their children. Holocultural and field studies tend to support this hypothesis. Katz and Konner (1981:195) found that father–infant proximity (degree of emotional warmth and physical proximity) is closest in gathering–hunting (gathered foods by females are principle resources, meat is secondary) populations and most distant in cultures where herding or advanced agriculture is practiced. In the latter, cattle, camels and land are considered the essential accumulable

resources necessary for survival. These findings are consistent with Whiting and Whiting's (1975) holocultural study of husband–wife intimacy. They found husband–wife intimacy to be greatest in cultures without accumulated resources or capital investments. While there are other factors to consider (e.g. protection of resources and polygyny rate), there is a strong tendency for fathers/husbands to devote more time to their children/wives if there are no accumulable resources.

Table 16.7 examines father availability in societies that have been investigated with systematic observations. The data support the holocultural findings that fathers in societies with accumulable resources are less likely to spend time near children than fathers in societies where there are few accumulable resources and where men contribute less to the diet than females.

Katz and Konner also found that in societies where hunting by men was the primary mode of subsistence (i.e. hunter–gatherers not gatherer–hunters), father–infant proximity was distant. This is consistent with recent field studies conducted among Ache foragers. Meat and honey collected by Ache men represent the majority of calories consumed (Hill and Kaplan, this volume (Chapter 17)), and Ache fathers hold their children on average only 10 minutes per day (Hill *et al.* 1985). This is the lowest amount of paternal holding recorded for a foraging population that has been quantitatively investigated; no other population where males contribute the majority of subsistence foods has been intensively investigated.

While the above hypothesis correctly predicts differences between intensive farmers and

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gathers, and between hunter-gatherers and gatherer-hunters, it is not useful in predicting intercultural variability among foraging populations where females contribute significantly to the diet (i.e. gatherer-hunters, such as Efe, !Kung and Australian Aborigines, and hunter-gatherers, such as Aka and Mbuti). Table 16.2 demonstrates some of the variability in direct paternal care of infants in systematically observed populations where females contribute significantly to the diet. Among the Efe and !Kung, females contribute substantially more calories than the men (Lee 1979, Peacock 1985), and Aka men and women contribute nearly equal amounts (Bahuchet 1987). Men in all three societies are not responsible for the majority of the calories consumed and there are no accumulable resources essential for survival. Consequently, a father's reproductive success in these societies may be enhanced by contributing more time to the direct care of infants than among the Ache fathers for instance. Females in these populations would also benefit by selecting males who would be willing and capable of doing childcare because the women are less dependent on men for subsistence. But the above hypothesis would predict that Aka fathers should spend less time with infants rather than more time as indicated, since they contribute more to subsistence than Efe or !Kung fathers.

Other evolutionary factors often cited as influencing the level of paternal investment are not useful in explaining intercultural variability among foragers where females contribute the majority of the resources. Paternity certainty, sex ratio and level of polygyny, are important factors for evolutionary biologists, but none of these factors help to explain why Aka fathers do substantially more direct caretaking than Efe or !Kung fathers. Based on blood analysis, paternity certainty is known to be above 95% for both !Kung and Aka, therefore it is not helpful in explaining differences in paternal care between these two groups. The sex ratio for individuals over 15 years of age is 0.86 for !Kung (Lee 1979:48), 1.10 for Efe (Bailey and Peacock 1987), and 0.90 for Aka. According to the sex ratio hypothesis, if there are many more adult males than adult females, as is found among the Yǎnomamö, then male-male competition for females is predicted to be greater and males contribute less to the direct care of infants, but the

Efe have the greatest number of males to females yet they do just as much infant holding as !Kung. Consequently, the sex-ratio hypothesis is not useful for these data.

Level of polygyny is also considered an important factor in predicting direct paternal care. In societies where levels of polygyny are high, direct care by fathers is predicted to be low because male-male competition is also expected to be higher, and if the father is polygynous he must divide his time between more children. But the Efe and !Kung levels of polygyny are much lower than the Aka (3–4% among Efe and !Kung versus 15% among the Aka); paternal infant care should be just the opposite of that which is found.

At this point, these factors do not help explain the extraordinary level of paternal investment found among the Aka. Two ecological factors unique to Aka and other pygmy net-hunters are more useful in understanding the behavior of Aka fathers. First, Aka females have to travel farther more regularly than either Efe or !Kung females. Aka females travel just as far as Aka males to participate in the net-hunt, about 8–20 kilometers per day. Efe women work for Lese farmers and !Kung females usually gather goods, in both cases usually not far from the camp. In both of these groups an older female sibling is often the preferred secondary caretaker, not the father as among the Aka. Aka fathers may be preferred over female siblings because of the greater distances traveled by Aka females. Older female siblings would not be able to carry infants for any great length of time on the net-hunt, whereas the father could.

The second unique feature of Aka culture is that male and female subsistence patterns overlap for the majority of the year. The net-hunt and caterpillar collecting are the predominant subsistence activities during the year and both are activities in which male and female subsistence activities overlap. Both Efe and !Kung have subsistence activities in which husband and wife participate together, but they are infrequent and generally involve gathering rather than hunting activities. Regular long-distance travel may explain why Aka fathers help with infant care on the net-hunt (Aka fathers do more infant caretaking on the net-hunt than Efe or !Kung fathers do in a camp setting), but male and female overlapping subsistence activity may be

an important factor in understanding why Aka fathers do so much more caretaking than !Kung or Efe in the camp setting.

It is difficult to identify precisely what mechanism(s) encourages greater direct paternal investment when husband and wife subsistence activities overlap. Mammals and especially humans are known for their propensity towards emotional attachment (Bowlby 1969). Aka fathers' extensive interaction and familiarity with their children may generate greater emotional attachment, and therefore greater concern and involvement in their children's well-being. The family is the basic economic unit, family members are more intimate than in most cultures (sleeping and 'working' together), and there is a need to have an adult secondary caretaker rather than an older sibling. Consequently, Aka fathers may be willing to invest more in offspring than what is necessary to maximize reproductive success.

This overview of intercultural variation suggests a pattern similar to that found in intracultural variation: generally, men will spend more time with their children when they have fewer resources to offer. An important way in which men may compete for matings is by accrual/expenditure of parental resources. Intraculturally, Aka fathers with more brothers have more resources available to them, and consequently, spend more time in activities such as status maintenance rather than in direct childcare. Aka fathers with no brothers and few resources spend considerably more time in the direct care of children. Interculturally, societies in which men accumulate essential resources (e.g. land or cattle) or contribute the majority of calories to the diet, spend significantly less time in the direct care of children than do men in societies where males contribute less to the diet than do females. Fathers in these societies have fewer resources to offer and therefore reproductive success is enhanced by contributing to the direct care of children. It is also to the female's reproductive advantage in such societies to select men that demonstrate the desire and ability to do direct childcare.

Summary

1. Darwin's (1871) and Bateman's (1948) prediction that where one sex benefits more by

multiple mating, one would expect more intrasexual competition, is supported by Aka demographic data: (a) Aka males ranged farther than Aka females; (b) Aka male mortality was greater than female mortality, especially when mating began (i.e. early adulthood); and, (c) Aka male reproductive variance was greater than female reproductive variance, and males were the more polygamous sex.

2. Distinctions in intrasexual competition between the relatively peaceful Aka 'forest' people and the 'fierce' Yānomamö are simply a matter of degree, being more pronounced among the 'fierce' people.
3. Sexual selection influences paternal investment patterns both intraculturally and intercultural. Generally, men will spend more time with their children when they have fewer resources to offer.
4. Evolutionary predictions were less useful in explaining why Aka fathers invested so much more time in the direct care of their infants in comparison to !Kung and Efe fathers. Male and female overlapping subsistence patterns and long-distance travel required by Aka females on the net-hunt appear to be critical factors.

Acknowledgements

Research for this chapter was supported by grants from the Wenner-Gren Foundation, University of California Humanities Fund, and the Swan Fund. I am indebted to the government of the Central African Republic, especially to Jean-Claude Kazagui, le Haut Commissaire de la Recherche Scientifique et Technologique, for facilitating the project. Etohe, Boseke, Samole, and Maman provided special insights into Aka parenting, and Justin Mongosso assisted tremendously with logistical advice. I also wish to acknowledge the useful comments of the editors of this volume, as well as Napoleon Chagnon, Donald Brown, Donald Symons, Jesus Cardozo, Michael Jochim, Serge Bahuchet and P. Herbert Leiderman on earlier drafts of this chapter.

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