Evidence for dominant wild female chimpanzees investing more in sons

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Abstract. Parents are expected to invest more resources in the offspring gender that promises more grandchildren. In a variety of vertebrate species skewed sex ratio at birth and differential parental investment in sons and daughters have been documented. Wild chimpanzees, *Pan troglodytes*, living in the Taï National Park, Côte d'Ivoire, were followed for 15 years. This community followed the typical species pattern in that males showed natal philopatry and the sex ratio at birth was almost 1:1. An analysis of 33 inter-birth intervals revealed that dominant females invested about 2 years more in sons, whereas subdominant females invested about 11 months more in daughters. The first difference is significant. Sons of dominant females had higher survival than other youngsters. The benefit of such a facultative investment is discussed. The absence of such a differential investment by mothers in other chimpanzee populations is compatible with an explanation based on variations within the female-biased dispersal pattern in this species and the possible role of maternal condition.

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The theory of parental investment predicts that parents should invest more resources in the offspring gender that promises more grandchildren (Hamilton 1967; Trivers & Willard 1973; Clutton-Brock 1991). In a variety of vertebrate species the sex ratio at birth is skewed and parents invest differentially in sons and daughters (Clark 1978; Altmann 1980; Clutton-Brock et al. 1984; Silk 1988; Gomendio et al. 1990; van Schaik & Hrdy 1991; Gowaty 1993; Holekamp & Smale 1995). These empirical observations are, however, difficult to explain as in some species more males are produced and in others more females. Much theoretical work has been devoted to explain how differential parental investment should evolve (Trivers & Willard 1973; Clark 1978; Silk 1983; Clutton-Brock 1991; Hiraiwa-Hasegawa 1993).

Several factors have been proposed to affect the parents' investment in one or the other sex in social vertebrates: maternal condition; competition between individuals over local resources; and individual dispersal patterns. Trivers & Willard (1973) predicted that mothers in good condition should bias investment towards offspring of the sex that is most likely to benefit from the mother's contribution. In polygynous vertebrates, breeding success in males is more strongly influenced by body size and condition than in females, and we should expect parents to invest more in sons when resources are plentiful and in daughters when they are scarce. As predicted, high maternal rank in red deer, *Cervus elaphus*, which guarantees access to better foraging places, is associated with more sons produced at birth and with higher reproductive success for sons than for daughters (Clutton-Brock et al. 1984).

In many social vertebrate species, one sex has a stronger tendency to disperse than the other (Pusey & Packer 1987; Gowaty 1993). Depending upon the conditions, members of one sex might compete or cooperate for food, and mothers might react to this circumstance (Clark 1978; Silk 1983). In cercopithecine primates with female philopatry, under conditions of intense competition for local resources, dominant females produce an excess of daughters. When the competitive conditions are weak, dominant females produce an excess of sons (van Schaik & Hrdy 1991). Under intense competition, daughters benefit dominant

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mothers as they serve as allies in competition with other matrilines, whereas they represent a liability to high-ranking mothers under weak competition (Altmann 1980).

In this paper, my aim was to investigate whether mothers among wild chimpanzee, *Pan troglodytes*, populations demonstrate a facultative adjustment of their investment in their offspring according to sex. Chimpanzees belong to the few primate species in which only females disperse between social groups (Pusey & Packer 1987). Previous studies in wild chimpanzees revealed no bias in either birth sex ratio or parental investment (Goodall 1986; Hiraiwa-Hasegawa 1990; Nishida et al. 1990). I first document the situation in Taï and then discuss how it might be explained by the present theoretical thinking on parental investment. The present analysis is based on 15 years of observations on the wild chimpanzees of the Taï National Park, Côte d'Ivoire.

METHODS

A community of chimpanzees in the Taï tropical rainforest (Côte d'Ivoire) has been studied since 1979, and all group members were identified by early 1982 (see Boesch & Boesch 1983, 1989 for more details). Since then we have followed the individuals on a regular basis, recording daily presence, birth and the sex of the newborn, and keeping track of all signs of illnesses or injuries. In 1982, the community included 78 chimpanzees, and in the following 13 years 70 births, 115 deaths and 20 female transfers were observed.

The total maternal investment in an infant was measured by the inter-birth interval, as maternal effort is expected to be proportional to the duration of subsequent inter-birth intervals (Silk 1988). The inter-birth interval, which includes the whole period during which a mother suckles and transports an infant, is the period between two consecutive births. I excluded the data if the mother or the infant died before weaning. Also, since spontaneous abortions and early miscarriages could not be recorded consistently, I did not take these events into account. Wild chimpanzees tend to isolate themselves when they give birth, but in 16 cases I could ascertain the date of birth within a few days. In 17 cases, I had to estimate it because the birth occurred either before the study started or when the mother was not seen

for 3–4 months. The average inter-birth interval for the estimated birth date was 69.59 months, whereas that for known birth dates was 68.56 months, indicating that my estimates did not produce a notable distortion.

I classified mothers as being either dominant or subdominant on the basis of priority of access to feeding places. This classification into only two dominance categories minimizes the impact of small changes in dominance rank and the impact of changes resulting from important demographic events. Ranks were stable enough during the study period that no individual female had to be moved between dominance categories. Age and dominance rank did not correlate in the females considered in this study.

Survival curves were produced from instantaneous life-tables (Caughley 1977) with known mothers. In this method, the sample size for each age class varies depending upon the number of individuals observed entering an age class within the chimpanzee community. Individuals that died from known unnatural causes (e.g. human snares) and infants that died following the death of their mother were excluded from these curves, since offspring less than 5 years old do not survive their mother's death. I analysed survival only up to 13 years, by when all females emigrated to other communities. I used the univariate chi-squares for the log rank test of the lifetest procedure (SAS 1989) to compare the different curves. Only data up to 1991 were included in the present analysis, because the mortality of the Taï chimpanzees between 1992 and 1995 was largely determined by the impact of two serious viral epidemics (Le Guenno et al. 1995; Formenty et al., in press). Including the data from these two periods eliminates all significant differences.
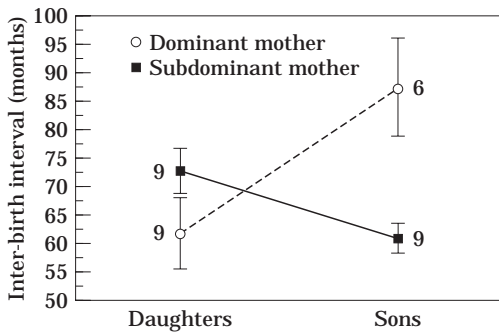
RESULTS

An analysis of 61 identified newborn babies in Taï chimpanzees (nine newborns died before we could determine their sex) revealed a sex ratio of 1:1.25 in favour of females, which does not deviate significantly from a birth sex ratio of 1:1.

The analysis of 33 inter-birth intervals in Taï chimpanzees revealed that the length of the maternal investment period was not affected when the rank of the mother or the sex of the infant were considered alone (Table I). Age of the mother had

Table I. Results of an analysis of covariance (GLM, SAS 1989) for the effects of sex and rank (factors) and age (covariate) on the inter-birth intervals in Taï chimpanzees ($N=33$)

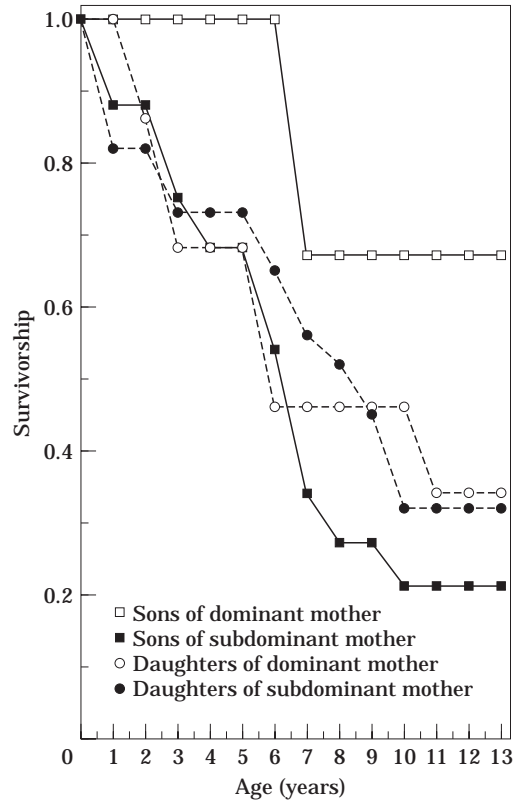|	F	df	P
Age of mother	4.46	1,28	<0.05
Sex of offspring	3.60	1,28	<0.1
Rank of mother	0.29	1,28	NS
Sex∗rank	19.47	1,28	0.0001

Inter-birth intervals were $\log_{10}$ transformed to normalize residuals. Type III sums of squares (partial SS) were used in the analysis, which corrects for each factor the effects of all the other factors.

Figure 1. Interaction plot of the effect of sex of the infant and rank of the mother on the length of the inter-birth interval (in months; standard errors and sample size are indicated for each point; $P<0.0001$). The average inter-birth interval was 69.1 months ($N=33$, range: 48–120 months).

Figure 2. Survivorship curves for the offspring of dominant and subdominant mothers in Taï chimpanzees (comparing sons' curves: $P\leqslant0.05$, all other comparisons: NS).

a small effect if corrected for both sex of the infant and rank of the mother. However, the combined effect of the rank of the mother and the sex of her offspring played a major role: dominant females invested about 2 years more in sons than in daughters, whereas subdominant females invested 11 months more in daughters than in sons (Fig. 1). Dominant mothers invested a similar amount of time in daughters as subdominant mothers invested in sons.

The 33 inter-birth intervals analysed were recorded from 19 females over a period of 25 years. Thus, some females contributed more than one inter-birth interval (seven females contributed two, three females three and one four inter-birth intervals). To test if this affected the result, I reanalysed the data by using only the first inter-

birth interval per female, if they contributed more than one for the same infant sex. This procedure reduced the sample size to 24 inter-birth intervals and produced the same significant differences (the combined effect of the rank of the mother and the sex of her offsprng remained significant at $P<0.002$).

Such differential investment by the mother makes sense only if the offspring benefits from it (Trivers & Willard 1973). One important fitness component of young chimpanzees is survival until adulthood. Figure 2 shows the survival of the two sexes according to the dominance status of their mother. Sons of dominant mothers had higher survival than those from subdominant mothers (univariate chi-square for log rank test: $P=0.05$) and the effect increased from 2 years of age onwards ($P<0.05$), but was not apparent within the first 5 years (NS). However, for daughters no

effect of differential investment by the mothers was seen (univariate chi-square for log rank test: NS). Dominant mothers invested 13 months more in their sons than subdominant mothers invested in their daughters (Fig. 1), and this supplementary year of investment may be required to improve offspring survival after infancy. These data do not make clear why subdominant mothers invest more time in daughters; it might be that the small sample size did not allow me to document a small but real effect on their survival. It was not possible to test for effects of parental investment on reproductive success of the offspring, because females left the community before reproducing and the high mortality rate observed since 1992 reduced our male sample size dramatically.

DISCUSSION

Taï chimpanzee mothers invested more in sons when they were dominant, and this increased their sons' survival. It seems impossible to explain the differential investment in sons by a higher cost of rearing sons, as chimpanzee males and females have the same birth weight and size, and grow at the same rate during the first 10 years of life (Gavan 1971). The present result mirrors results obtained in cercopithecine primates under conditions of intense local resource competition (van Schaik & Hrdy 1991), the difference in sex-biased investment being explained by the opposite dispersal patterns: where macaques are expected to invest in philopatric daughters, chimpanzees are expected to invest in philopatric sons. Were Taï chimpanzees living under intense local resource competition? Some empirical data might support this. Growth rate has been suggested to reflect the intensity of food competition (van Schaik & Hrdy 1991). During the study period, the community's annual population growth rate was negative (C. Boesch & H. Boesch, unpublished data). However, Taï chimpanzees also suffered from leopard, *Panthera pardus*, predation during this period (Boesch 1991), which also contributed to this negative trend. The number of adult males in the community varied between six and nine and the adult sex ratio was constantly equal to or smaller than 1:3 (C. Boesch & H. Boesch, unpublished data), which shows high reproductive potentials for the males and might indicate strong competition for mates between males. All other things being equal, the higher survival rate of sons of dominant mothers would guarantee them more grandchildren than lower ranking mothers. The longer inter-birth intervals, at the same time, limit the intensity of the conflicts between siblings. If, in addition, surviving sons of dominant mothers achieve higher social status and higher reproductive success, the longer maternal investment we observed in Taï chimpanzees would be even more adaptive. But as yet, no data are available to support these last two expectations.

Why is there no similar trend in other chimpanzee populations? Female dispersal is generally observed in chimpanzees but varies in intensity between populations. In Taï, 88% of the females transferred between communities at adolescence. In Gombe National Park in Tanzania, only 13% of the females transferred and the benefit attributed to dominant mothers when investing in sons seems to be compensated by the important affiliative and supportive interactions observed between mothers and daughters (Goodall 1986), rendering daughters an ally rather than a competitor (such a 'local resource enhancement' argument was used to explain male-biased sex ratios in birds with 'helpers at the nest' (Gowaty & Lennartz 1985) and female-biased sex ratios in dominant mothers among cercopithecine primates with intense local resource competition (van Schaik & Hrdy 1991)). In Mahale National Park in Tanzania, all daughters disperse but no difference has been documented in the inter-birth interval (Nishida et al. 1990; T. Nishida, personal communication). Perhaps maternal investment after infancy is also required to guarantee higher reproductive success of the sons. In Mahale, females are known to transfer more than once, and in 17% of the cases they left their juvenile offspring behind before transferring to a new group and were, therefore, not able to provide any additional support (Nishida et al. 1990).

In Taï chimpanzees, maternal investment seems to be influenced by the sex-biased dispersal pattern and maternal conditions. The difference observed in maternal investment between chimpanzee populations might similarly be explained by differential adjustment of mothers to a varying degree of sex-biased dispersal and to the possible effect of maternal investment. The optimal strategy for chimpanzee mothers appears, therefore, to vary between populations.

ACKNOWLEDGMENTS

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