

Furtive mating in female chimpanzees

It has been assumed for more than 30 years that in chimpanzee communities the observed social unit and the reproductive unit are identical. We present genetic evidence that female chimpanzees seek to mate outside their own social group. We have studied a community of West African chimpanzees in which half the offspring were sired by non-community males.

Chimpanzees live in social groups of between 20 and 100 animals. Males remain in their community and defend home ranges of 7–30 km², whereas females disperse at around the time of puberty (10–12 years of age)^{1,2}. Most matings are promiscuous and opportunistic, but some are restricted by a dominant male and others may be exclusive, with couples leaving on a 'consortship' for several days or weeks^{1–3}. Inferring dates of conception is difficult as females are sexually active throughout their 15-day oestrus, and the gestation period has been shown to be variable⁴. Many questions about chimpanzee reproduction and female mating strategies remain unanswered.

Using non-invasive genetic methods⁵, we investigated reproductive behaviour in a community of West African *Pan troglodytes verus* from the Tai Forest, Ivory Coast (Fig. 1). The group has been studied for 17 years and has been fully habituated to human presence for over 10 years⁶. Both sexes interact continuously throughout most of the day, but at night each adult builds a tree-top nest and sleeps alone. The Tai community lives on a 25 km² territory surrounded by five non-habituated communities.

Between 1991 and 1995 we collected hair samples from nests and buccal-cell samples from chewed fruit, from which we

Table 1 Paternity of 14 infants in the Tai chimpanzee community

Offspring	Paternity				Behavioural data		
	Mother	Microsatellite genotypes		Number of loci	Absence during oestrus (days)		Consortship with male
		Father	Paternity exclusion probability		8 months before birth	7–9 months before birth	
LYCHEE	LOUKOUM	Macho	0.926	11	no data	no data	
Cacao	CASTOR	Fitz	0.887	9	15*	40*	Fitz
DORRY	DILLY	Kendo	0.967	10	1	3	
FEDORA	FOSSEY	Fitz	0.950	10	8	17	Fitz, Kendo
Gargantua	GOMA	Brutus	0.956	9	0	0	
Papot	PERLA	Rousseau	0.924	10	8	15	
VANILLE	VENUS	Ali	0.941	11	3	19	
PANDORA	PERLA	EGP		10	2	2	
BAGHEERA	BELLE	EGP		11	1	16	
Congo	CASTOR	EGP		11	2	11	
Hector	HERA	EGP		11	15*	45*	
HELENE	HERA	EGP		6	15*	45*	Macho, Brutus
Lefkas	LOUKOUM	EGP		8	1	1	
MOGNIE	MYSTERE	EGP		10	5	26	Kendo

The name of the likely father (sharing common alleles at all 11 loci) from the same community is indicated. The probability of excluding a randomly sampled male from the same population using the same loci and allele frequencies is given. High probabilities indicate correct identification. Conception was estimated to have occurred 229±30 days before birth⁴. EGP, extra-group paternity. Females, upper case; males, lower case.
*Females completely absent throughout an oestrus were assigned an oestrus duration of 15 days per month.

extracted DNA of all 52 community members. We genotyped 21 mother–infant pairs and 11 potential fathers at 11 microsatellite loci. For 13 infants we tested all potential community fathers, and in seven cases all community males could be excluded. These infants must have been sired by males from other communities (Table 1).

All seven females who bore infants sired outside the group left the community during part of their oestrus period around the inferred time of conception (Table 1). This behaviour is surreptitious, and four of these seven were absent for only one or two days during the most probable conception period. Furthermore, during 17 years of observation we have never seen adult females approach neighbouring community males outside confrontational contexts. We witnessed several permanent transfers by foreign females to the study community but no surreptitious visits. As inter-community fights are the only opportunity for females to observe foreign males, the question arises as to whether females choose non-group mates on the basis of their performance during such encounters.

The females that have offspring with non-community males did not spend more time outside the group than females who conceived with group males. Thus, from the perspective of a male, a temporary absence from the group of a female during oestrus does not reliably indicate the extra-group paternity of group-born offspring. This is important as males may kill infants conceived outside their community².

Much significance has been attributed to consortships for male reproductive success^{1–3}. In this study, only two of six consortships resulted in paternity (Table 1). Also, a positive correlation between male

dominance rank and reproductive success in primates has often been suggested⁷. Small sample size precludes statistical tests of the association between male rank and reproductive success in the Tai Forest; however, four of the 11 potential fathers in our study were dominant males but only two of these sired infants during their tenure. Brutus and Macho (dominant for 10 and 1.5 years, respectively) sired no infants while dominant, but each sired one offspring afterwards. On the other hand, individuals that held dominant status for some time in their lives sired more than two-thirds of the offspring for which we identified likely fathers. Our results show that infants sired with neighbouring community females must be included when estimating male reproductive success.

Years of direct observation have supported the assumption that chimpanzees mate primarily within their social community, just as observations of supposedly monogamous birds did not reveal the significance of extra-pair copulations⁸. Possible cases of extra-group matings in chimpanzees were known¹ and in two cases (Gombe and Bossou)^{5,9} detected genetically, but the behaviour was dismissed as insignificant. Our data suggest otherwise, and underscore the need for comparable genetic surveys of other populations (now underway at Tai).

The significance of female-biased gene flow on chimpanzee social structure and evolution has been documented¹⁰. Our results show a further consequence of female behaviour, extra-group paternity, must now be taken into account when interpreting estimates of gene flow and genetic distance. That mate choice can occur within a larger area than the traditionally observed social units has implica-

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Figure 1 Tai chimpanzees grooming.

tions not only for the evolution of mating systems and sociality, but also for the management of viable populations of these threatened primates.

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Four climate cycles in Vostok ice core

The Russian–American and French international effort for drilling in ice achieved both a technical and a scientific success by reaching a depth of 3,350 m at the Russian Vostok station (78° S, 106° E; elevation 3,488 m; mean temperature –55 °C). In addition to being the deepest ice core, the Vostok core is now believed to cover the past four glacial–interglacial cycles (~400,000 years), a surprisingly long climate sequence which will be a valuable tool for palaeoclimatologists.

Hole number 5 started from the surface in 1990 and reached 2,755 m at the end of January 1994 (ref. 1). The station had to be closed for the winter because of financial and technical difficulties, but reopened the following summer season. Drilling operations were restarted and continued through the 1995 winter by three Russian drillers (headed by N. Vassiliev). By January 1996, the drilling had reached 3,350 m, but again was stopped because the station had to close for the winter.

The first 2,755-m-deep ice core had already provided the longest undisturbed ice climate record (Fig. 1). Studies of the deuterium (δD ; a proxy for temperature), dust and $\delta^{18}O$ records clearly showed that this core covers almost two full climate cycles^{1,2} (~240,000 years). The ice was processed during the 1995–96 field season for electrical conductivity measurements (ECM). Apart from volcanic events, the

background ECM signal is linked to acid concentration, and therefore depends on the balance between cation and anion concentrations. This changes dramatically between glacial and interglacial times as a result of changes in the intensity in sources of marine and continental aerosols and/or changes in their transport by atmospheric circulation^{3–5}. High conductivity (acidity) is observed for the last interglacial ice (marine stage 5.5) as well as for the three warm substages of stage 7, whereas the signal appears lower for stage 6 and cold substages of stage 7. Despite noticeable differences, ECM gives a stratigraphy consistent with that provided by the isotope record.

Below 2,755 m, we observe two long intervals of sustained high electrical conductivity, at 3,073–3,124 m and 3,262–3,298 m depth in the core. We believe that these correspond to interglacial stages 9 and 11, respectively. This is confirmed by deuterium data as well as by preliminary dust measurements, which both fall between Holocene and last interglacial levels. An ice layer at 3,020–3,035 m has a similar ‘interglacial’ ECM signal but no clear deuterium signature in stable isotopes, possibly because of the insufficient time resolution at this period. Warm marine substages 9.1 and 9.3 may correspond to intervals 3,020–3,035 m and 3,073–3,124 m, respectively. For ice

deeper than 3,124 m, the ECM fine structure (with patterns also depending on cation and anion concentrations; I. B., manuscript in preparation) suggests that the high dust input of glacial stage 10 started at 3,139 m. This level, dated to 340,000 years in the SPECMAP chronology⁶, should mark the boundary between stages 9.3 and 10. The interval 3,139–3,250 m probably corresponds to cold stage 10 and the high, short ECM event around 3,180 m results from a high aerosol concentration. Before warm stage 11 (below 3,298 m), the deep ice close to 3,350 m displays a low ECM signal, low deuterium content and high dust concentrations. This deepest part was thus probably deposited at the end of the previous glacial period (that is, at stage 12).

For a very preliminary age estimate, we assume that the ice layers thin linearly with depth below 2,755 m (240,000 years ago) and adopt an age of 340,000 years at 3,139 m depth. Although simple, this approach appears reasonable: age at 3,030 m (310,000 years) is consistent with stage 9.1; ages at 3,262 and 3,298 m (385,000 and 400,000 years) are more or less in agreement with stage 11, and 426,000 years at 3,350 m is consistent with the end of stage 12.

A wealth of climate-related information will be soon available back to 400,000 years or so ago. The period from 240,000–400,000 years is recorded in about 600 m of ice, which will allow us to study it with high resolution: 1 m of ice would represent 200 years at 2,755 m, 260 at 3,000 m and 450 at 3,300 m. Current measurements include the crystalline texture of the ice, the isotopic composition and concentration of aerosols, chemical constituents and cosmogenic isotopes, as well as the elemental and isotopic composition of the entrapped air bubbles. The last 300 m of ice to be drilled (drilling will be stopped 50 m above the water lake⁷) may have the potential to extend the climate sequence still further back in time, although disturbances of the layers, as seen for the deep ice in the Greenland ice core, are likely to appear.

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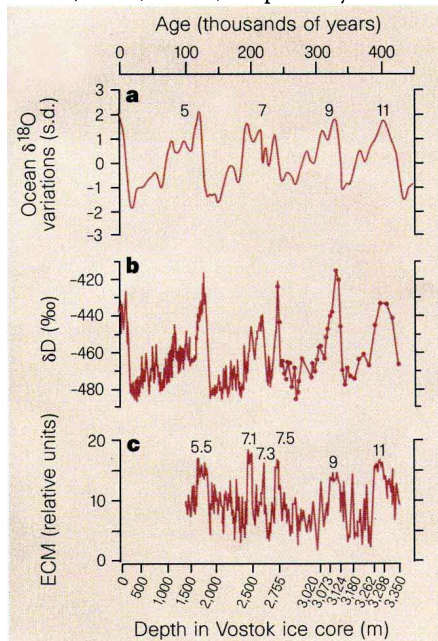


Figure 1 Vostok and marine climate records over the past 400,000 years. **a**, Ocean $\delta^{18}O$ variations (standard deviation units) deduced from foraminifera data from deep-sea cores (SPECMAP stacked record from Imbrie *et al.*⁶). **b**, Vostok δD values (expressed as ‰ with respect to Standard Mean Ocean Water). The continuous deuterium profile down to 2,755 m is from Jouzel *et al.*¹ and from a discontinuous set of samples below this depth. **c**, Vostok ECM signal (3-m running mean and expressed in relative units) for depth below 1,500 m. Numbers indicate marine stages.