



Female reproductive strategies, paternity and community structure in wild West African chimpanzees

PASCAL GAGNEUX*†, CHRISTOPHE BOESCH* & DAVID S. WOODRUFF†

*Zoologisches Institut Universität Basel

†Department of Biology and Center for Molecular Genetics, University of California, San Diego

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Although the variability and complexity of chimpanzee behaviour frustrates generalization, it is widely believed that social evolution in this species occurs in the context of the recognizable social group or community. We used a combination of field observations and noninvasive genotyping to study the genetic structure of a habituated community of 55 wild chimpanzees, *Pan troglodytes verus*, in the Taï Forest, Côte d'Ivoire. Pedigree relationships in that community show that female mate choice strategies are more variable than previously supposed and that the observed social groups are not the exclusive reproductive units. Genetic evidence based on nuclear microsatellite markers and behavioural observations reveal that females in the Taï forest actively seek mating partners outside their social unit; noncommunity males accounted for half the paternities over 5 years. This female mating strategy increases male gene flow between communities despite male philopatry, and negates the predicted higher relatedness among community males. Kin selection seems unlikely to explain the frequent cooperation and sharing observed among group males in this population. Similarly, inbreeding avoidance is probably not the sole cause of permanent adolescent female dispersal as a combination of extragroup mating and avoidance of incest with home group males would allow females to avoid inbreeding without the hazards associated with immigration into a new community. Extragroup mating as part of chimpanzee females' reproductive strategy may allow them to choose from a wider variety and number of males, without losing the resources and support provided by their male social group partners.

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Studying animal mating behaviour from a female perspective has provided new insights into the evolution of mating systems (Gowaty 1992, 1997). The revelation of widespread extrapair matings in situations traditionally viewed as exclusively monogamous (e.g. Westneat et al. 1990; Gullberg et al. 1992; Palombit 1994; Reichard 1995) has contributed to the on-going re-examination of the simplistic sexual selection caricature of promiscuous males and discriminating, coy females (Darwin 1859, 1871; Hrdy & Williams 1983; Hrdy 1986; Andersson 1994). It is now appreciated that females of many species actively seek to mate with multiple males. The benefits to the female can be material (adequate sperm supply and increased paternal care) and genetic (providing a wider choice of good genes, a compensation for low mate fertility, and an increased opportunity to avoid genetic incompatibilities; Zeh & Zeh 1996, 1997). The question

arises as to whether females in species with larger, physically dominant males are restricted in their future mate choices if they form reproductive and social bonds with a particular male or group of males (Smuts 1993; Mesnick 1997). The potential for future mate choice will be most restricted in such cases for long-lived species where resident males stay reproductively active for many breeding seasons and the turnover of males is low. Such a situation prevails in the chimpanzees, *Pan troglodytes*, the subjects of this investigation.

In primates, especially in species living in multimale groups such as chimpanzees, females actively solicit matings with many different group males. However, trying to choose mates outside her social group might jeopardize the resources guaranteed to a female and her offspring by her current male partners. Perhaps the only way for such females to gain access to a larger number of males without risking retaliation from their male social group partners is through furtively seeking out extragroup, nonresident males in nearby territories. Our results suggest that female chimpanzees may behave in accordance with this prediction.

Correspondence: P. Gagneux, Department of Biology, University of California, San Diego, La Jolla, CA 92093-0116, U.S.A. (email: gagneux@biomail.ucsd.edu). C. Boesch is at the Zoologisches Institut Universität Basel, Rheinsprung 9, 4051 Basel, Switzerland.

Our knowledge of wild chimpanzees is based on field research at different sites across Africa (Goodall 1968, 1971, 1986; Nishida 1968, 1979, 1990; Ghiglieri 1984; Chapman & Wrangham 1993; Boesch 1996). These studies show that chimpanzees live in fission–fusion social groups called communities whose members form smaller transient parties that remain stable for periods of a few minutes to days. In this paper we employ the terms ‘party’, ‘community’ and ‘regional population’ to denote three hierarchical levels of social and spatial organization (and use the terms social group and community as synonyms). The community or unit-group is widely regarded as the fundamental social unit in this species (Goodall 1986; Nishida 1990). Communities typically comprise 20–100 individuals and defend home ranges of 7–30 km². At study sites across Africa, males stay in their natal community and cooperate in territory defence against neighbouring communities. Females, in contrast, usually disperse at 10–12 years of age, around the time they reach sexual maturity. Where contiguous habitat still exists, as at Mahale, Tanzania and Taï, Côte d’Ivoire, most females disperse (Nishida 1990; Boesch 1997).

The variability of chimpanzee mating systems is well documented (Tutin 1979; Goodall 1986; Hasegawa & Hiraiwa-Hasegawa 1990; Morin 1993); three female mating situations are widely recognized and some evidence points to the existence of a fourth. We use the phrase female ‘mating situation’ instead of the conventional phrase ‘mating strategy’ as the first three situations may not involve actual female choice; the degree to which females are able to choose their mates is unclear as the physically stronger males can force them to copulate and even coerce them to enter into a consortship (Goodall 1986). In the first type of situation, matings occur in a group setting and can be characterized as promiscuous. The majority of matings are of this type. Second, restrictive mating, with a dominant male monopolizing access to a particular female, can also occur in group settings, especially during the peak anogenital swelling period of the female cycle. The third mating situation, also apparently exclusive, occurs between an adult pair when the couple leaves the community as a consortship for a period of several days to weeks. In all three mating situations, the larger size and greater strength of adult males allows them to dominate every female on a one-on-one basis. A fourth mating situation is suggested by field observations that individual females occasionally disappear from their social groups for a few days. It is possible, although it has never been observed, that such females may mate furtively with males from nearby communities. For example, mature females of *Pan t. schweinfurthii* at Gombe, Tanzania, have been observed transferring temporarily to neighbouring communities or visiting before returning to their natal community to both mate and give birth (Pusey 1979; Tutin 1980; Tutin & McGinnis 1981; Goodall 1986). Similar visits by adult females were observed between two study groups in Mahale, Tanzania (Uehara 1981; Nishida et al. 1985; Hasegawa 1989), although most coincided with the extinction of one of the two study groups. Such observations, suggestive of a fourth female mating situation,

raise the possibility that the social group or community, the focus of almost all behavioural studies, may not represent the actual reproductive unit. Our goal was to examine the genetic relationships of individuals in a well-studied group to determine whether there was any evidence for the occurrence of the extragroup matings.

A combination of factors explain why, despite decades of field work, important questions about mate choice, paternity and reproductive success in chimpanzees remain unanswered. Inferring precise dates of conception in the field is very difficult as female sexual activity and associated anogenital swellings last throughout the 15-day oestrus around monthly ovulation. Furthermore, the gestation period in chimpanzees is highly variable (Martin 1992) and it remains unclear whether this is due to variability in the timing of ovulation with respect to exterior signs, or to differential sperm survival after copulation. Similarly, whether male chimpanzee can identify the precise time of ovulation remains unknown although they keep close track of a cycling female’s oestrous stage by frequently inspecting her genitals, and competition among males increases around the time of peak swelling. There is good evidence for the dissociation of swelling and ovulation as newly immigrating females have been observed to keep their swelling for more than a month and pregnant females often produce swellings (Goodall 1986; Hasegawa & Hiraiwa-Hasegawa 1990; Nishida 1990; Wallis 1992, 1993, 1997; C. Boesch & H. Boesch, unpublished data). As detumescent females of neighbouring groups may be attacked, and often fatally wounded (Goodall et al. 1979; Nishida & Hiraiwa-Hasegawa 1985), oestrous swellings are clearly important for a female’s acceptance by males of other communities during transfer at adolescence and visits, and could give females the possibility of manipulating their social acceptance by males as well as the probability of fertilization. Whether, and to what degree females are capable of such manipulation remains to be determined. The fact that younger females, and females of lower social status, show more swellings during pregnancy and postpartum also suggests that swellings may be used as a social tool (Nishida 1990; Wallis 1993; C. Boesch & H. Boesch, unpublished data). Another feature that confounds the simple interpretation of chimpanzee mating behaviour is the existence of copulatory plugs, which are typically good indicators of strong sperm competition (Dixson & Mundy 1994). The same authors also report large variability in penis length, a feature that could enable some males to remove the plug left by others. Finally, it should be noted that females can interrupt copulation by rapidly moving away from the male shortly before ejaculation (C. Boesch, personal observation). All of these facts preclude a simple association between copulatory behaviour and probability of paternity.

The coupling of noninvasive genotyping methods with traditional observational studies allows us to circumvent such uncertainties and establish formal genetic relationships within communities of wild chimpanzees without necessitating darting- or trapping-based biopsy (Morin & Woodruff 1992, 1996; Woodruff 1993; Morin et al. 1994a, b). Using such methods, we have been able to

investigate reproductive behaviour in a habituated community of West African *Pan t. verus* that has been observed for the last 17 years in the Taï National Park, Côte d'Ivoire (Boesch & Boesch 1989, 1990). Taï forest chimpanzees form very cohesive communities in which both sexes interact more frequently than they do in comparable communities of *P. t. schweinfurthii*. During the daylight, males were observed in association with females 82% of the time (Boesch 1996). The mean diadic association index between particular males and females (the amount of time a male and a female are observed together, i.e. as part of the same travelling party, over the total time each of the two has been observed) was 12% at Taï compared with 7% in Gombe, and an estimated 5% at Mahale (Goodall 1986; Nishida 1990; C. Boesch, unpublished data). At night, each adult builds a new tree-top nest and sleeps alone. The Taï-habituated community defends a territory of ca. 25 km² surrounded by five nonhabituated communities occupying contiguous areas. All 55 members of this one community are individually recognizable and all mother–offspring relationships were confirmed by long-term follows.

Our preliminary analyses of the Taï-habituated community suggested a high incidence of extragroup paternity (EGP) (Gagneux et al. 1997a). Here we present the detailed report of our observations and analyses of paternity and relatedness. We also discuss the effects of the female strategy of extragroup mating on the observed genetic structure in this study community and its significance with respect to female dispersal behaviour. Finally, we consider the possibility that extragroup mating is a more general phenomenon in chimpanzees, and we examine its implications for their evolution and conservation.

METHODS

We collected DNA samples from all individuals in the Taï community in 1990–1995 and examined 21 mother–infant pairs (five mothers with two offspring each, 11 with a single offspring), three orphans (two of them adopted by adult males), and 11 potential fathers (defined here as community males ≥ 9 years old at time of conception; Tutin 1979; Nishida 1990). Fifty-two individuals were genotyped at each of 11 polymorphic nuclear microsatellite loci. The loci used were dinucleotide repeats *Mfd3*, *Mfd18*, *Mfd23*, *Mfd32*, and *LL1*, trinucleotide repeats *FABP* and *PLA2A*, and tetranucleotide repeats *RENA4*, *FESPS*, *MBP2* and *vWF* (Kimpton et al. 1992; Polymeropoulos et al. 1992a, b; Morin et al. 1994b). All are described as perfect repeats in *H. sapiens*. Most of the DNA samples consisted of shed (telogen) hairs collected in recognizable individuals' night nests. We followed known individuals until they built their sleeping nests in trees 10–40 m above ground, and we collected the hairs from the nest early the following morning after observing the same individual leaving it. For nine individuals, it was also possible to collect discarded freshly masticated pulp wadges of fruits as a source of buccal cells (fruits of the large tropical tree *Saccoglottis gabonensis*). In addition, plucked hair and a single bone were available from four

individuals that died of natural causes. Of the 24 offspring sampled, we sampled 21 independently, and three from their mother's nest (chimpanzees share their mother's nest for up to 5 years). We collected all hairs wearing latex gloves to avoid human contamination. We placed each hair individually in a paper envelope and stored it at ambient temperature in a dry box containing regularly desiccated silica gel.

We made DNA extractions from single hairs in the laboratory at the University of California, San Diego. For shed hair, we used simple Chelex extractions, and for wadge and bone samples we used the QIAamp tissue extraction kit (QIAGEN). We amplified 11 nuclear loci using the polymerase chain reaction (PCR) following the method described by Morin et al. (1994b). The reliability of the genotypes was tested by repeated amplification of all loci and by confirmation that all mother–infant pairs shared a common allele at all loci (there were no maternal exclusions). We considered the genotype for each individual at each locus reliable only when three independent amplifications using two different hairs yielded the same result for homozygotes, or when a heterozygote was detected with two different hair extracts in two different amplifications (Gagneux et al. 1997b). For all mother–offspring pairs, we ascertained the genotype of each individual by analysing independent samples from nests in which the mother and/or offspring slept alone as well as from nests of the same mother with two different infants, or from wadges chewed only by one individual.

To test for the possibility of null alleles and allelic dropout, we conducted paternity exclusions using only those loci at which the offspring and the father were heterozygous. Null alleles occur when a mutation in the primer binding region, flanking a particular microsatellite locus prevents the amplification of the allele during the PCR (Pemberton et al. 1995). Allelic dropout results from preferential amplification of only one of the two alleles in PCR with extremely small template quantity (Walsh et al. 1992). In the seven EGP cases described below, all community males were still excluded, indicating that the exclusions were not caused by null alleles or allelic dropout. We tested all extraction solutions (5% Chelex, Biorad) by amplifying two blanks per batch of extractions. For each PCR, we tested the reagents with a negative control using deionized water as a template, as well as a positive control consisting of extract from P.G.'s arm hair. For four of the 11 loci shared between humans and chimpanzees, P.G.'s alleles differed in size from the chimpanzee alleles, providing an effective control for the most likely source of human contamination.

We then used the individual multilocus genotypes, consisting of up to 22 alleles, to calculate paternity exclusion probabilities (following Chakraborty et al. 1988) using a computer program compiled by Geffen (cited in Girman et al. 1997). We verified all paternity exclusions by manually aligning the genotypes of mother, offspring and all possible community fathers. We used the same microsatellite genotypes to calculate the mean coefficient of relatedness, *R*, among males and females in the Taï community. We calculated *R* using Queller & Goodnight's KINSHIP program (Queller &

Goodnight 1994) and Geffen's KINPOP program. We estimated standard deviations for relatedness values by jackknifing over all loci following Sokal & Rohlf (1981, pp. 796–797). We used all males and all females for the mean R calculations. We also calculated mean R for a subset of older males, all born prior to 1984.

The observational data consisted of presence–absence records collected during whole-day focal animal follows lasting from shortly before sunrise to nightfall. Throughout the course of the day, we recorded the presence of all community members and the oestrous stage of females. An individual was considered absent if it was not sighted during the day by any of the Tai group's experienced observers. Absence thus does not prove absence from the group's territory but rather absence of social interactions with the community members being followed. Even individuals recorded as 'present' on any given day could theoretically leave the community and the territory for short periods of time (1–6 h), especially when the community foraged near the boundaries of its territory.

RESULTS

The multilocus genotypes of all community members together with allele numbers and frequencies are shown in Table 1 and 2. For a total of 55 individuals, 35 could be replicably genotyped at all 11 loci, nine at only 10, five at only nine, and three at only eight loci. The three youngest offspring (sampled in their mother's nest only) could not be genotyped because the very low quantity of template DNA in their small hairs resulted in unsuccessful amplification (mean of less than 4 ng of DNA in an extraction from a single shed hair, in contrast to >20 ng of DNA from a plucked hair, as measured by fluorescence on a Perceptive Biosystems multiplate reader using Pico Green dye from Molecular Probes).

We used these multilocus genotypes to conduct paternity exclusions for 21 of 24 offspring (Table 3). We were able to test all potential fathers in this community for 13 offspring and could exclude all males in seven cases. Thus, about half of these offspring (seven of 13 offspring from six females) must have been sired by noncommunity males. For one of the seven EGP offspring (Lefkas), a group male (Kendo) was excluded at a single locus only; we cannot exclude the possibility that this was due to a single mutation in Kendo, but as the mutation rate of microsatellite loci is ca. 10^{-4} – 10^{-5} per gamete per generation (Bruford & Wayne 1993), it is improbable. In the other six cases, where a probable father was identified in the habituated community, we calculated the probability of excluding a randomly sampled male from the Tai Forest chimpanzee population to which this particular community belongs (considering this community as a representative sample of the local forest chimpanzee population). Paternity exclusion probabilities were 0.89–0.96 (Table 4). For three of these six offspring, more loci will have to be genotyped to obtain paternity exclusion probabilities of 95%. In these three cases, even though likely fathers were identified within the community, we could not exclude the possibility that nongroup males sired the offspring. Age of the likely fathers in the group

for these six cases ranged from 12 (Ali) to about 40 years (Brutus). For the remaining eight older offspring, we were not able to genotype all potential fathers in the community as some had died before they could be sampled. However, one likely father (Macho, not excluded at any locus, paternity exclusion probability: 0.926) was identified for one of these offspring (Lychee), resulting in a total of seven offspring with likely paternity in the group versus seven offspring sired by outside males. We conclude that EGP is an important part of the local mating system.

In the two cases of adoption by two adult males that we were able to genotype, neither one sired their adoptive son (for the adopted juveniles Ali and Brando, Brutus and Ulysse were excluded as fathers at three and five loci, respectively). Both young males had lost their mothers shortly after weaning and were then adopted by an adult male. Adoption here means all association between an infant and an adult similar to that seen between infants and their mothers. The adoptive fathers showed some maternal behaviours including waiting for the juvenile to catch up during group travel, providing social support during agonistic interactions with other group members, and food sharing.

All females that conceived outside the community were absent for one whole day or more during the most probable time of conception. For each adult female, we counted the number of days she was absent from the community during the three periods of oestrus around conception. Although the most probable time of conception was 8 months (ca. 230 days) prior to birth, we also considered a second longer period lasting 7–9 months before birth, as conception is less probable but not impossible in the seventh and ninth month before birth (Martin 1992). All seven females impregnated elsewhere were absent from this habituated community during part of their period of oestrus around the inferred date of conception. The duration of individual absences ranged from 1 to 21 days. Strikingly, four of these seven females fertilized by noncommunity males were away for only 1–2 days during the most probable period of conception.

Interestingly, five of the six females that conceived with habituated group males were also absent for some days around their inferred date of conception. Females, that mated with noncommunity males did not spend more time away from the group than females that conceived with group males (Table 4). Thus from a male's perspective, a female's temporary absence from the community during oestrus is not a reliable predictor of the paternity of offspring subsequently born within the community. This is important as observations at Mahale suggest (Nishida & Kawanaka 1985) that males are capable of selective infanticide when they perceive extragroup paternity to have occurred.

Relatedness calculations revealed no significant difference in relatedness between the sexes (Fig. 1). Both sexes had the mean pairwise relatedness of unrelated individuals. Two males (Kendo and Fitz), which also succeeded each other as alpha males, were maternal brothers, as judged from observations of their interactions with their mother, as well as genetic data (identical mitochondrial

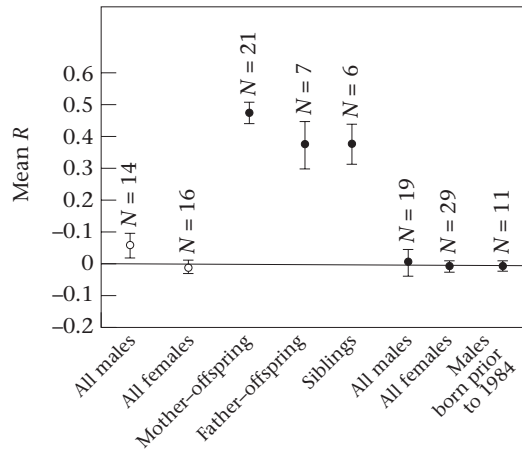


Figure 1. Mean (\pm SE) coefficient of relatedness values for different classes of individuals of the Tai community (\bullet) based on genotypes at 11 microsatellite loci. For comparison, we present the values for the Gombe community (\circ), based on a subset of eight loci (data: Morin et al. 1994b). Standard errors were estimated by jackknifing over all loci following Sokal & Rohlf (1981).

haplotypes and $R=0.3 \pm 0.106$; unpublished data). The mean coefficient of relatedness among mother-offspring pairs was 0.48 ± 0.03 , which did not differ significantly from the expected value of 0.5. The value among sibling pairs of 0.36 ± 0.07 probably reflects the inclusion of half-sibling pairs.

DISCUSSION

Our results suggest that female chimpanzee mate choice strategies require reassessment. The fact that chimpanzees belonging to neighbouring communities are not habituated to the presence of researchers might explain why furtive encounters between receptive group females and neighbouring males, as well as between receptive neighbouring (unhabituated) females and group males, have never been observed. The secretive nature of this female mating behaviour is underscored by the fact that during 17 years of observation, adult females were never seen approaching males from neighbouring communities except in direct confrontational contexts involving the whole group or party, during which mating was not observed and agonistic behaviour dominated.

Our genetic observations shed new light on several aspects of chimpanzee reproductive behaviour, including the significance of consortships and individual rank in determining reproductive success and the possibility that inbreeding avoidance is the prime cause of female dispersal. First, although much significance has been attributed to consortships for male reproductive success at Gombe (Tutin 1979, 1980; Goodall 1986), researchers at Mahale report no such significance (Hasegawa & Hiraiwa-Hasegawa 1990). At Tai, we found that only two of the 14 paternities were likely to have resulted from an observed consortship (Fitz and Castor, Fitz and Fossey, two out of six consortships, see Table 4). Significantly, two of the seven EGP cases also involved females that entered consortships for 1–7 days with habituated community males

during the relevant period of oestrus. In light of the four unproductive within-group consortships, the question arises whether consortships could be used by males to promote their future as well as immediate reproductive success by strengthening special relationships with particular females, even if the particular consortship does not result in paternity. Special relationships or friendships between males and females have been observed on several occasions at Tai (C. Boesch, unpublished data). A comparison of individual male reproductive success while in the group and while on consortship will have to await additional data. The fact that the two successful consortships documented here involved the same male (Fitz) illustrates the potential importance of individuality or character for determining differences in mating strategies in these apes.

Second, a positive association between a male primate's rank in a community's dominance hierarchy and his reproductive success has been reported in numerous behavioural studies (e.g. Colishaw & Dunbar 1991). In the case of chimpanzees, however, field observations provide only weak and circumstantial support for such an association (Tutin 1975; Hasegawa & Hiraiwa-Hasegawa 1983, 1990; Takasaki 1985; Kawanaka 1990). A strong correlation between mating frequencies of dominant males with particular females and the females' oestrus stage has been reported (Hasegawa & Hiraiwa-Hasegawa 1990) but without proof of paternity other than inference from copulation frequency. Of the 11 potential fathers in the Tai community, four were dominant (alpha) males but only two of these, Kendo and Fitz, sired infants during their tenure. Brutus, the alpha male for 10 years, and Macho, the alpha male for 1.5 years, sired none of the surviving offspring during their tenure. However, they each sired one offspring after they lost alpha status. These results suggest a weak positive association between alpha status at some point in a male's life and reproductive success but our small sample size precludes more precise conclusions. More importantly, our study shows that one must include infants sired with neighbouring community females when estimating an individual male's reproductive success. Eventually, studies including neighbouring chimpanzee communities will permit the assessment of the importance of male rank for female choice and reproductive success across social units.

Third, in chimpanzees, inbreeding avoidance is widely accepted as the underlying factor responsible for dispersal by adolescent females (Goodall 1968; Pusey 1979, 1980) although same-sex competition for mates and for resources have also been invoked (Moore & Rauf 1984; Moore 1993). Our results suggest that females could avoid inbreeding without dispersing as adolescents by using a combination mate choice strategy: actively mating with noncommunity males and avoiding close kin within their own community. The latter behaviour is known to occur, as active avoidance of matings between mothers and sons as well as between siblings has been documented (Pusey 1979; Tutin 1980). Younger females have also been reported to avoid mating with older males (old enough to have fathered a female 10–12 years old; Goodall 1986), which may be a way of avoiding incest with their

Table 1. Genotypes of the Tai community

Individual	Loci											
	FABP	PLA2A	Mfd3	Mfd18	Mfd23	Mfd32	MBP2	vWF	RENA4	FESPS	LL1	
Brutus	6	7	8	5	8	11	1	5	1	1	3	9
Darwin	7	4	9	5	8	12	1	1	1	2	3	7
Fitz	6	1	11	5	8	9	4	5	1	1	3	4
Kendo	2	6	9	6	8	13	1	3	2	2	3	4
Macho	6	4	9	5	10	11	1	4	1	2	3	4
Rousseau	2	6	3	5	12	10	3	5	2	2	9	9
Ulysse	7	7	9	6	8	9	5	5	2	2	8	9
Brando	7	4	4	5	11	14	1	4	1	2	3	3
Ali	5	6	9	6	10	10	4	5	1	2	8	10
Gipsy	6	4	3	5	6	10	5	5	1	2	5	8
Marius	3	6	11	6	10	13	1	1	2	2	3	4
Sartre	3	6	1	6	7	8	3	5	1	2	2	5
AGATHE	3	3	4	6	10	8	2	4	1	2	2	4
ELLE	6	6	8	6	8	11	5	5	2	2	3	8
BAGHERA	5	6	8	10	9	13	2	4	2	1	2	2
BIJOU	6	7	9	6	13	14	4	4	1	2	5	8
CASTOR	4	6	3	6	8	12	4	4	1	2	4	8
Congo	2	4	3	5	8	14	4	4	2	2	4	4
Cacao	4	6	3	4	11	14	4	4	1	2	3	4
DILLY	6	6	9	5	15	9	2	3	1	2	7	8
DORY*	2	6	9	5	8	9	1	3	2	2	3	7
FANNY	6	6	11	6	10	13	2	4	1	2	3	5
FOSSEY*	2	6	11	5	9	11	1	4	2	2	5	9
FEDORA	6	6	10	5	11	13	1	4	2	2	5	9
GALA	5	5	9	5	13	9	1	4	1	2	3	9
GITANE	4	6	3	5	12	10	1	5	1	2	8	8
GOYAVE	6	6	4	5	12	13	1	1	2	2	5	8
GOMA	6	7	7	5	10	13	2	4	2	2	3	8
Gargantua	6	6	6	5	8	13	1	2	1	2	3	3
HERA	5	6	9	5	13	11	4	5	1	2	4	8
Hector*	6	6	9	6	10	13	3	5	1	2	3	8

Table 1. Continued

Individual	Loci																	
	FABP	PLA2A	Mfd3	Mfd18	Mfd23	Mfd32	MBP2	vWF	RENA4	FESPS	LL1							
HELENE	5	6	3	11	6	11	10	13	11	12	5	5	3	4	1	2	4	8
KANA*	6	7	4	11	3	5	9	10	10	13	5	5	3	4	1	2	4	8
LOUKOUM	4	7	1	4	5	6	8	12	10	11	4	4	3	4	2	2	4	8
LEFKAS*	4	7	4	4	5	6	8	8	10	14	4	5	4	5	2	2	4	6
LYCHEE	4	6	4	4	6	10	8	12	10	11	1	4	4	4	2	2	4	8
MYSTERE	6	7	2	6	5	6	8	14	10	14	1	4	3	6	2	2	4	8
MOGNIÉ*	3	7	6	6	5	6	9	14	10	14	1	4	4	6	2	2	4	4
ONDINE	4	7	4	5	8	11	5	15	11	13	3	4	3	5	1	2	4	4
SIRENE*	6	7	4	4	5	10	8	12	11	11	1	4	3	6	2	2	4	9
PERLA	6	6	4	6	6	10	8	11	9	14	4	4	3	4	2	2	4	8
Papot*	6	6	4	5	3	11	8	11	11	14	4	5	3	4	2	2	4	8
PANDORA	6	7	4	6	6	10	8	12	13	14	2	4	4	4	1	2	4	9
POUPEE	6	6	2	6	5	6	9	9	10	16	4	4	4	4	1	2	4	9
RICCI	4	4	4	5	8	11	8	15	11	13	3	4	3	5	1	2	4	10
Nino	4	7	4	4	8	9	5	15	12	13	1	3	5	9	1	2	4	6
SALOME	6	6	1	1	3	11	8	9	11	14	5	6	4	5	1	2	6	6
VENUS*	6	6	1	4	8	11	6	12	12	13	5	6	3	4	2	2	3	5
VANILLE*	6	6	4	4	8	9	6	8	13	14	4	6	4	4	2	2	3	10
XERES	6	6	1	1	9	9	6	7	11	12	1	4	4	6	2	2	5	8
XINDRA	3	6	1	1	8	9	5	6	7	11	12	4	4	6	2	2	5	8
ZERLINA	2	7	4	4	8	8	6	8	14	11	4	4	5	6	2	2	4	4
Author P.G.	1	6	11	10	4	8	3	9	8	13	1	4	7	8	5	10	1	12
Size of allele	201	68	129	82	89	90	89	89	90	120	120	126	126	254	126	126	80	80
Repeat unit	3 bp	3 bp	2 bp	2 bp	2 bp	2 bp	2 bp	2 bp	2 bp	4 bp	4 bp	4 bp	4 bp	4 bp	4 bp	4 bp	2 bp	2 bp

Alleles for each locus are numbered starting with the smallest allele, each increment equals one repeat unit. Names of females are capitalized; names of males have initial capital letters only. Offspring/juvenile names in italics.

*DNA extracted from hair and wadge.

Table 2. Alleles, allele frequencies and heterozygosity

Locus	Allele	Count	Frequency	SE	Expected heterozygosity
<i>FABP</i>	204	6	0.0588	0.025	0.678
	207	6	0.0588	0.025	
	210	11	0.1078	0.033	
	213	6	0.0588	0.025	
	216	53	0.5196	0.054	
	219	17	0.1667	0.04	
<i>PLA2A</i>	222	3	0.0294	0.018	0.627
	68	21	0.2059	0.043	
	71	2	0.0196	0.015	
	77	49	0.4804	0.054	
	80	12	0.1176	0.035	
<i>Mfd3</i>	83	18	0.1765	0.041	0.777
	133	12	0.1224	0.036	
	139	5	0.051	0.024	
	141	2	0.0204	0.015	
	143	16	0.1633	0.04	
	145	25	0.2551	0.048	
	147	1	0.0102	0.011	
	149	34	0.3469	0.052	
<i>Mfd18</i>	151	3	0.0306	0.019	0.69
	86	2	0.0196	0.015	
	90	43	0.4216	0.055	
	92	35	0.3431	0.052	
	94	2	0.0196	0.015	
	98	2	0.0196	0.015	
<i>Mfd23</i>	100	17	0.1667	0.041	0.853
	102	1	0.0098	0.011	
	99	4	0.0392	0.021	
	101	2	0.0196	0.015	
	103	30	0.2941	0.05	
	105	8	0.0784	0.029	
	107	6	0.0588	0.026	
	109	11	0.1078	0.034	
	111	11	0.1078	0.034	
	113	14	0.1373	0.038	
	115	7	0.0686	0.028	
	117	7	0.0686	0.028	
	119	2	0.0196	0.015	
<i>Mfd32</i>	104	1	0.0098	0.011	0.813
	106	7	0.0686	0.028	
	108	14	0.1373	0.039	
	110	27	0.2647	0.05	
	112	8	0.0784	0.03	
	114	27	0.2647	0.05	
	116	16	0.1569	0.041	
	120	2	0.0196	0.016	
<i>LL1</i>	82	3	0.0294	0.02	0.833
	84	20	0.1961	0.046	
	86	25	0.2451	0.05	
	88	9	0.0882	0.033	
	90	4	0.0392	0.023	
	92	3	0.0294	0.02	
	94	23	0.2255	0.049	
	96	12	0.1176	0.037	
	98	3	0.0294	0.02	
	<i>MBP2</i>	120	21	0.21	
124		8	0.08	0.031	
128		9	0.09	0.032	
132		35	0.35	0.054	
136		24	0.24	0.048	
140		3	0.03	0.019	
<i>vWF</i>	126	3	0.0306	0.019	0.683
	134	28	0.2857	0.05	
	138	46	0.4694	0.055	
	142	11	0.1122	0.035	
	146	9	0.0918	0.032	
	158	1	0.0102	0.011	
	126	29	0.3021	0.057	
130	67	0.6979	0.057		
<i>RENA4</i>	254	28	0.3415	0.058	0.455
	258	54	0.6585	0.058	

Table 3. Paternity exclusions for most infants alive between 1991 and 1995 in the Tai chimpanzee community*

Mother	Offspring	Potential fathers											Number of group males not sampled				
		Brutus	Macho	Kendo	Fitz	Darwin	Rousseau	Ulysse	Ali	Gipsy	Sartre	Marius					
All group males sampled	CASTOR***	>1	>1	1	NE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	FEDORA	>1	>1	>1	NE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	FOSSEY	>1	>1	NE	1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	DILLY	>1	>1	1	1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	VENUS	>1	>1	1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	GOMA	NE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	PERLA	>1	>1	>1	>1	>1	NE	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	BELLE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	BAGHEERA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	Congo	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	CASTOR	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	Hector	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	HERA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	HERA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	LOUKOUM	>1	>1	1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	MYSTERE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	PANDORA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	PERLA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	
	LOUKOUM	>1	NE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4
	LYCHEE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4
Nino	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
RICCI	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	7	
FANNY	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
Marius	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
GOYAVE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
GITANE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	6	
GITANE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	3	
Gipsy	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	6	
SIRENE	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	6	
SALOME	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
XERES	1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
XINDRA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	6	
Ali	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	6	
No sample	Brando	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	4	
No sample	KANA	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	>1	3	

Names of females are capitalized; names of males have initial capital letters only.

Potential fathers: NE: not excluded at any locus; 1: males excluded at a single locus only; >1: males excluded at more than one locus. The first four potential fathers represent four sequential alpha males over the period from 1982 to 1995.

*Three of the 24 infants living during this period could not be tested because DNA could not be successfully extracted from the hair samples.

†Males were only included as potential fathers if they had reached the age of 9 years by the inferred time of conception (Pusey 1979; Tutin 1979; Goodall 1986).

Table 4. Paternity for 14 infants for the Tai Forest chimpanzee community

Offspring	Paternity (Microsatellite genotypes)			Behavioural data (Absence during different oestrous periods*)				Status of father
	Mother	Father†	Paternity exclusion probability	Number of loci	Birth date	8 months before birth‡	7–9 months before birth	
LYCHEE	LOUKOUM	Macho	0.926	11	1 Mar. 1986	No data	No data	ex-alpha
Cacao	CASTOR	Fitz	0.887	9	14 Mar. 1994	15§	40§	alpha
DORRY	DILLY	Kendo	0.967	10	24 Nov. 1991	1	3	alpha
FEDORA	FOSSEY	Fitz	0.950	10	12 Nov. 1991	8	17	alpha
Gargantua	GOMA	Brutus	0.956	9	21 Sep. 1991	0	0	alpha
Papot	PERLA	Rousseau	0.924	10	19 Nov. 1989	8	15	ex-alpha
VANILLE	VENUS	Ali	0.941	11	30 May 1991	3	19	
PANDORA	PERLA	EGP		10	2 Sep. 1995	2	2	
BAGHEERA	BELLE	EGP		11	18 Sep. 1994	1	16	
Congo	CASTOR	EGP		11	28 Jan. 1992	2	11	
Hector	HERA	EGP		11	10 Dec. 1990	15§	45§	
Helene	HERA	EGP		8	4 Aug. 1995	15§	45§	Macho and Brutus
Lefkas	LOUKOUM	EGP		8	7 Oct. 1991	1	1	
MOGNIE	MYSTERE	EGP		10	31 Jul. 1990	5	26	Kendo

For each mother-offspring pair, the name of the likely father is indicated if he was a member of the same group. EGP (extra group paternity) was demonstrated in seven cases for which all group males were excluded. Exclusion probability stands for the probability of excluding a randomly sampled male from the same population using the same loci and allele frequencies. *Absence: number of days (diurnal periods) the mother was absent from the group (not seen for the entire day) during oestrus 8 months and 7–9 months prior to the birth of her young. Females that conceived with extra group males did not spend more time outside the group than females that conceived with group males (two-tailed *t* test for the oestrous period 8 months before birth as well as the three oestrous periods 7–9 months before birth: $df=10$, $P>0.67$). †Father: males were excluded as the father if they did not possess a common allele with the offspring at one of the 11 loci. All unexcluded males shared an allele with their offspring at every locus considered.

‡Conception was estimated to have occurred 229 ± 30 days before birth (Martin 1992).

§Females completely absent throughout oestrus were assigned an oestrus duration of 15 days/month.

apparently unknown fathers. A combined female mating strategy involving extragroup mating behaviour would avoid the physical and social costs associated with dispersal. Young females may have to spend long periods of time travelling and feeding alone in unknown territory, making them highly vulnerable to predation by leopards, and subsequently have to win acceptance into a new community in the face of much hostility from resident females (Alberts & Altmann 1995). If our results have any generality, then inbreeding avoidance alone is unlikely to account for sex-biased dispersal in chimpanzees.

The question of whether extragroup mating is more important in west Africa than elsewhere is open to investigation. Geographical differences in behaviour are known and DNA-sequence based measures of genetic distance between western *P. t. verus* and central and eastern *P. t. troglodytes* and *P. t. schweinfurthii* are large (Morin et al. 1994a, 1995; P. Gagneux, D. S. Woodruff & C. Boesch, unpublished data). As noted above, males and females interact more continuously in the Taï Forest than they do in East African communities. Taï chimpanzees live in a bisexually bonded social system rather than a male bonded system as observed at Gombe (Boesch 1996). The degree to which these differences are affected primarily by one factor, food abundance (Chapman & Wrangham 1993; Wrangham et al. 1996), as opposed to multiple factors including predation pressure, hunting rate, and opportunities for mating as well as food abundance (Boesch 1991, 1996), is still debated.

We considered the possibility that the observed female extragroup mating strategy is a consequence of special circumstances. The Taï community experienced a gradual decline in size from 86 to 55 individuals between 1979 and 1990, and then a sudden population decline from 55 to 35 individuals due to two epizootics of Ebola virus in 1992 and 1994. The most dramatic decline in numbers during the two Ebola epizootics (leading to a possible shortage of males in a community with an adult male: female ratio of ca. 1:4) does not account for the high incidence of EGP, however, as four of seven cases predate the first Ebola outbreak. Also, the dates of conception for the seven cases of EGP are temporally spread out between 1990 and 1995. As a test of the possible impact of demographic decline, we calculated the mean relatedness coefficient for the 11 adult and subadult males born prior to 1984 (Fig. 1); it was not higher than that of the females, leading us to the conclusion that the existence of substantial male gene flow between the study group and adjacent groups predates the demographic decline.

Two comparable genetic studies involving the Kasakela community in Gombe and the Bossou community in Guinea corroborate the Taï result and suggest that extragroup mating is a part of the typical chimpanzee mating system. At Gombe, two males from the neighbouring Mitumba community could not be excluded as fathers of Kasakela community-born offspring (Morin et al. 1994b). In the case of Bossou, there is genetic evidence that one study-group infant was fathered by a noncommunity member (Sugiyama et al. 1993). Clearly, genetic studies of communities surrounding habituated social groups are

now needed to characterize better this increasingly complex mating system.

For the Gombe Kasakela community, Morin et al. (1994a) reported a higher relatedness among males than among females. They concluded that this difference was a direct consequence of adolescent female dispersal behaviour and speculated that it could account for the evolution of male cooperation and sociality based on kin selection theory. Similarly, based on observations of female dispersal, Hasegawa (1989) refers to the males in the M group at Mahale as members of a kin group. At the outset of the present study we hypothesized that males at Taï were likely to be even more closely related, as female dispersal there is more common (over 88% of females dispersing versus 13% at Gombe; Boesch 1997; Goodall 1986). Also the degree of cooperation among males, especially during hunting for *Colobus badius* monkeys, far surpasses that observed at Gombe (Boesch 1994). One of the consequences of the high EGP rate, however, is that in addition to almost universal female dispersal, female behaviour mediates male gene flow between communities. The expected increase in male sex-biased relatedness within a social group is thus prevented by hitherto unrecognized outbreeding. The low mean relatedness among males may also reflect the fact that the adult males in the 1990–1995 population represent less than half of their age-cohort (11 out of 20 males born between 1970 and 1980 had died) and that they sired only three male offspring in the group, resulting in fewer male relatives than expected. The different results found at Gombe may indicate that EGP is less common there, possibly because opportunities for EGP in that more isolated community are much lower than at Taï, where the study community is still surrounded by five different communities. The apparent differences in male relatedness in these two communities is striking and merits re-examination.

The high frequency of EGP at Taï suggests the observed chimpanzee social unit does not correspond to the reproductive unit for either males or females. Furtive extragroup mating might be the only way for females to exercise mate choice after having committed to a community, given that community males, especially alpha males, dominate resident females. This reproductive strategy could allow females to expand the pool of males from which they choose fathers of their offspring without risking the loss of support and protection provided by their adult life-long male social partners. Such support is especially important in this species where lactation lasts up to 4 years and maternal care is very demanding.

Our results concur with genetic studies of other vertebrate species where the proportion of extrapair paternities are higher than suggested by observational data (Birkhead & Møller 1992; Sillero-Zubiri et al. 1996) and where females appear to initiate many of the extrapair copulations (Smith 1988; Gowaty & Bridges 1991; Gray 1997). Although mating systems are composed of the strategies of both sexes, as well as various counterstrategies (Hrdy & Williams 1983; Hrdy 1997), only the combination of behavioural observation with genetic methods enables us to demonstrate just how flexible the mating strategies of

both sexes really are in various taxa. For example, the recent discoveries that male Ethiopian wolves, *Canis simensis*, and Toque macaques, *Macaca sinica*, sire offspring outside their social groups, shows that, as in chimpanzees, the social and mating units are not necessarily identical (Sillero-Zubiri et al. 1996; Keane et al. 1997). Similarly, the allegedly monogamous gibbons are now known to engage in extrapair copulations as well as serial monogamy (Palombit 1994; Reichard 1995; Brockelman et al. 1998). That mate choice in chimpanzees can occur within a larger population than the traditionally observed social groups has important implications for the evolution of mating systems and sociality. The social pattern seen in females may partly result from constraints put on them by male territorial behaviour. The discrete social organization of chimpanzees and other primates into communities or groups could represent the most visible part of a social system, which in reality, is much more continuous.

Our observations have implications for the future evolution of chimpanzees. Female mating behaviour of the kind reported here will become more dangerous or impossible in increasingly fragmented habitats in Africa, and isolated chimpanzee communities are likely to suffer genetic erosion as gene flow is curtailed (Woodruff 1992). This curtailment of natural behaviours will exacerbate the negative impacts of range fragmentation and demographic collapse on this species' endangerment. Although managers in the future may be tempted to recreate the natural behaviours that affect gene flow by the artificial translocation of individual chimpanzees, this may be counterproductive because of the risks of spreading infectious diseases. Finally, we note that in captive situations, the difficulty of keeping multimale groups has artificially precluded the type of female mate choice reported here.

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References

- Alberts, S. C. & Altmann, J. 1995. Balancing costs and opportunities: dispersal in male baboons. *American Naturalist*, **145**, 279–306.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Birkhead, T. F. & Møller, P. 1992. *Sperm Competition in Birds*. New York: Academic Press.
- Boesch, C. 1991. The effect of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, **117**, 220–242.
- Boesch, C. 1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour*, **48**, 653–667.
- Boesch, C. 1996. Social grouping in Tai chimpanzees. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 101–113. Cambridge: Cambridge University Press.
- Boesch, C. 1997. Evidence for dominant wild female chimpanzees investing more in sons. *Animal Behaviour*, **54**, 811–815.
- Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, **78**, 547–573.
- Boesch, C. & Boesch, H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatologica*, **54**, 86–99.
- Brockelman, W. Y., Reichard, U., Treesucon, U. & Raemaekers, J. J. 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, **42**, 329–339.
- Bruford, M. W. & Wayne, R. K. 1993. Microsatellites and their application to population genetic studies. *Current Biology*, **3**, 939–943.
- Chakraborty, R., Meagher, T. W. & Smouse, P. E. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. *Genetics*, **118**, 527–536.
- Chapman, C. A. & Wrangham, R. W. 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *American Journal of Primatology*, **31**, 263–273.
- Colishaw, G. & Dunbar, R. I. M. 1991. Dominance and mating success in male primates. *Animal Behaviour*, **41**, 1045–1056.
- Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. London: J. Murray.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: J. Murray.
- Dixon, A. F. & Mundy, N. I. 1994. Sexual behaviour, sexual swelling, and penile evolution in chimpanzees (*Pan troglodytes*). *Archives of Sexual Behaviour*, **23**, 267–280.
- Gagneux, P., Woodruff, D. S. & Boesch, C. 1997a. Furtive mating by female chimpanzees. *Nature*, **387**, 327–328.
- Gagneux, P., Boesch, C. & Woodruff, D. S. 1997b. Microsatellite scoring errors associated with non-invasive genotyping based on nuclear DNA amplified from shed hair. *Molecular Ecology*, **6**, 861–868.
- Ghiglieri, M. P. 1984. *The Chimpanzees of the Kibale Forest: A Field Study of Ecology and Social Structure*. New York: Columbia University Press.
- Girman, D., Mills, G., Geffen, E. & Wayne, R. K. 1997. A molecular genetic analysis of social structure, dispersal, and pack interactions in the African wild dog (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, **40**, 187–198.
- Goodall, J. 1968. The behaviour of free living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, **1**, 163–311.
- Goodall, J. 1971. *In the Shadow of Man*. London: Collins.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.
- Goodall, J., Bandora, A., Bergman, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. Cown), pp. 13–53. Menlo Park: Benjamin/Cummings.
- Gowaty, P. A. 1992. Evolutionary biology and feminism. *Human Nature*, **3**, 217–249.
- Gowaty, P. A. 1997. Darwinian feminists and feminist evolutionists. In: *Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers* (Ed. by P. A. Gowaty), pp. 1–17. New York: Chapman & Hall.
- Gowaty, P. A. & Bridges, W. C. 1991. Behavioral, demographic and environmental correlates of extra-pair fertilizations in eastern bluebirds, *Sialia sialia*. *Behavioral Ecology*, **2**, 339–350.

- Gray, E. 1997. Do female red-winged blackbirds benefit genetically from seeking extra-pair copulations? *Animal Behaviour*, **53**, 605–623.
- Gullberg, A., Tegelström, H. & Gelter, H. P. 1992. DNA fingerprinting reveals multiple paternity in families of great and blue tits (*Parus major* and *P. caeruleus*). *Hereditas*, **117**, 103–108.
- Hasegawa, T. 1989. Sexual behavior of immigrant and resident female chimpanzees at Mahale. In: *Understanding Chimpanzees* (Ed. by P. Heltne & L. Marquardt), pp. 90–103. Cambridge, Massachusetts: Harvard University Press.
- Hasegawa, T. & Hiraiwa-Hasegawa, M. 1983. Opportunistic and restrictive matings among wild chimpanzees in the Mahale Mountains, Tanzania. *Journal of Ethology*, **1**, 75–85.
- Hasegawa, T. & Hiraiwa-Hasegawa, M. 1990. Sperm competition and mating behavior. In: *The Chimpanzees of the Mahale Mountains* (Ed. by T. Nishida), pp. 115–132. Tokyo: University Press of Tokyo.
- Hrdy, S. B. 1986. Empathy, polyandry, and the myth of the coy female. In: *Feminist Approaches to Science* (Ed. by R. Blerer), pp. 119–146. New York: Pergamon Press.
- Hrdy, S. B. 1997. Raising Darwin's consciousness; female sexuality and the prehuman origins of patriarchy. *Human Nature*, **8**, 1–48.
- Hrdy, S. B. & Williams, G. C. 1983. Behavioral biology and the double standard. In: *Social Behavior of Female Vertebrates* (Ed. S. K. Wasser), pp. 3–17. New York: Academic Press.
- Kawanaka, K. 1990. Alpha males' interactions and social skills. In: *The Chimpanzees of the Mahale Mountains* (Ed. by T. Nishida), pp. 171–188. Tokyo: University Press of Tokyo.
- Keane, B., Dittus, W. P. J. & Melnick, D. J. 1997. Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka, using molecular markers. *Molecular Ecology*, **6**, 267–282.
- Kimpton, C., Walton, A. & Gill, P. 1992. A further tetranucleotide repeat polymorphism in the *vWF* gene. *Human Molecular Genetics*, **1**, 287.
- Martin, R. D. 1992. Female cycles in relation to paternity in primate societies. In: *Paternity in Primates: Genetic Tests and Theories* (Ed. by R. D. Martin, A. F. Dixson & E. J. Wickings), pp. 238–274. Basel: Karger.
- Mesnick, S. L. 1997. Sexual alliances: evidence and evolutionary implications. In: *Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers* (Ed. by P. A. Gowaty), pp. 207–260. New York: Chapman & Hall.
- Moore, J. J. 1993. Inbreeding and outbreeding in primates: what's wrong with the dispersing sex? In: *The Natural History of Inbreeding and Outbreeding* (Ed. by N. W. Thornhill), pp. 392–426. Chicago: University of Chicago Press.
- Moore, J. J. & Rauf, A. 1984. Are dispersal and inbreeding avoidance related? *Animal Behaviour*, **32**, 94–112.
- Morin, P. A. 1993. Reproductive strategies in chimpanzees. *Yearbook of Physical Anthropology*, **36**, 179–212.
- Morin, P. A. & Woodruff, D. S. 1992. Paternity exclusion using multiple hypervariable microsatellite loci amplified from nuclear DNA of hair cells. In: *Paternity in Primates: Genetic Tests and Theories* (Ed. by R. D. Martin, A. F. Dixson & E. J. Wickings), pp. 63–81. Basel: Karger.
- Morin, P. A. & Woodruff, D. S. 1996. Non-invasive genotyping for vertebrate conservation. In: *Molecular Genetic Approaches in Conservation* (Ed. by T. B. Smith & R. K. Wayne), pp. 298–313. New York: Oxford University Press.
- Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J. & Woodruff, D. S. 1994a. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science*, **265**, 1193–1201.
- Morin, P. A., Wallis, J., Moore, J. J. & Woodruff, D. S. 1994b. Paternity exclusion in a community of wild chimpanzees using hypervariable simple sequence repeats. *Molecular Ecology*, **3**, 469–478.
- Morin, P. A., Moore, J. J. & Woodruff, D. S. 1995. Chimpanzee kinship. *Science*, **268**, 186–188.
- Nishida, T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates*, **9**, 167–224.
- Nishida, T. 1979. The social structure of chimpanzees of the Mahale Mountains. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. Cown), pp. 73–121. Menlo Park: Benjamin/Cummings.
- Nishida, T. 1990. Demography and reproductive profiles. In: *The Chimpanzees of the Mahale Mountains* (Ed. by T. Nishida), pp. 63–97. Tokyo: University Press of Tokyo.
- Nishida, T. & Hiraiwa-Hasegawa, M. 1985. Responses to a stranger mother-son pair in the wild chimpanzee: a case report. *Primates*, **26**, 1–13.
- Nishida, T. & Kawanaka, K. 1985. Within-group cannibalism by adult male chimpanzees. *Primates*, **26**, 274–284.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, T. & Takahata, Y. 1985. Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Zeitschrift für Tierpsychologie*, **67**, 284–301.
- Palombit, R. 1994. Dynamic pair bonds in hylobatids: implications regarding monogamous social systems. *Behaviour*, **128**, 65–101.
- Pemberton, J. M., Slate, J., Bancroft, D. R. & Barrett, J. A. 1995. Nonamplifying alleles at microsatellite loci: a caution for parentage and population studies. *Molecular Ecology*, **4**, 249–252.
- Polymeropoulos, M. H., Xiao, H. & Merrill, C. R. 1992a. Tetranucleotide repeat polymorphism at the human myelin basic protein gene (*MBP*). *Human Molecular Genetics*, **1**, 658.
- Polymeropoulos, M. H., Xiao, H. & Merrill, C. R. 1992b. Tetranucleotide repeat polymorphism at the human *c-fes/fps* proto-oncogene (*FES*). *Nucleic Acids Research*, **19**, 4018.
- Pusey, A. E. 1979. Intercommunity transfer of chimpanzees in Gombe National Park. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. McCrown), pp. 465–480. Menlo Park: Benjamin/Cummings.
- Pusey, A. E. 1980. Inbreeding avoidance in chimpanzees. *Animal Behaviour*, **28**, 543–552.
- Queller, D. C. & Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.
- Reichard, U. 1995. Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology*, **6**, 181–225.
- Sillero-Zubiri, C., Gotelli, D. & Macdonald, D. W. 1996. Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behavioral Ecology and Sociobiology*, **38**, 331–340.
- Smith, S. M. 1988. Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour*, **197**, 14–23.
- Smuts, B. B. 1993. Male aggression and sexual coercion of females in non-human primates and other mammals: evidence and theoretical implications. In: *Advances in the Study of Behavior* (Ed. by P. J. B. Slater, J. S. Rosenblatt, M. Milinski & C. T. Snowdon), pp. 1–63. New York: Academic Press.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. New York: W. H. Freeman.
- Sugiyama, Y., Kawamoto, S., Takenaka, O., Kumazaki, K. & Miwa, N. 1993. Paternity discrimination and inter-group relationships of chimpanzees at Bossou. *Primates*, **34**, 545–552.
- Takasaki, H. 1985. Female life history and mating patterns among M Group chimpanzees of the Mahale Mountains National Park, Tanzania. *Primates*, **26**, 121–129.
- Tutin, C. E. G. 1975. Exceptions to promiscuity in a feral chimpanzee community. In: *Contemporary Primatology* (Ed. by S. Kondo, M. Kawai & A. Ehara), pp. 445–449. Basel: Karger.
- Tutin, C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees. *Behavioral Ecology and Sociobiology*, **6**, 29–38.
- Tutin, C. E. G. 1980. Reproductive behaviour of wild chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility*, **28**, 43–57.

- Tutin, C. E. G. & McGinnis, P. R.** 1981. Chimpanzee reproduction in the wild. In: *Reproductive Biology of the Great Apes* (Ed. by C. E. Graham), pp. 239–264. New York: Academic Press.
- Uehara, S.** 1981. The social unit of wild chimpanzees: a reconsideration based on the diachronic data accumulated at Kasoje in the Mahale Mountains, Tanzania. *Afurika Kenkyu (Journal of African Studies)*, **20**, 15–32.
- Wallis, J.** 1992. Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *American Journal of Primatology*, **28**, 101–113.
- Wallis, J.** 1993. Anogenital swelling in pregnant chimpanzees of Gombe National Park. *American Journal of Primatology*, **31**, 89–98.
- Wallis, J.** 1997. A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, **109**, 297–307.
- Walsh, P. S., Ehrlich, H. A. & Higuchi, R.** 1992. Preferential amplification of alleles: mechanisms and solutions. *PCR Methods and Applications*, **1**, 241–250.
- Westneat, D. F., Sherman, P. W. & Morton, M. L.** 1990. The ecology and evolution of extra-pair copulation in birds. In: *Current Ornithology* (Ed. by D. M. Power), pp. 331–369. London: Plenum Press.
- Woodruff, D. S.** 1992. Genetics and the conservation of animals in fragmented habitats. In: *In Harmony with Nature* (Ed. by Y. S. Kheong & L. S. Win), pp. 258–272. Kuala Lumpur: Malay Nature Society.
- Woodruff, D. S.** 1993. Non-invasive genotyping of primates. *Primates*, **34**, 333–346.
- Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P. & Isabirye-Basuta, G.** 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 45–57. Cambridge: Cambridge University Press.
- Zeh, J. A. & Zeh, D. W.** 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **263**, 1711–1717.
- Zeh, J. A. & Zeh, D. W.** 1997. The evolution of polyandry II: post-copulatory defences against genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **264**, 69–75.