Male bimaturism and reproductive success in Sumatran orang-utans

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Although orang-utans live solitary lives most of the time, they have a complex social structure and are characterized by extreme sexual dimorphism. However, whereas some adult male orang-utans develop full secondary sexual characteristics, such as cheek flanges, others may stay in an ''arrested'' unflanged condition for up to 20 years after reaching sexual maturity. The result is a marked bimaturism among adult males. Flanged males allow females to overlap with their home range and often tolerate the presence of unflanged males. However, wherever possible flanged males actively prevent unflanged males from copulating with females. Two competing hypotheses, previously untested, have been advanced to explain male reproductive behavior and bimaturism in orang-utans: (1) the ''range-guardian'' hypothesis, which asserts that the flanged males are postreproductive and defend a range in which they tolerate sexually active, unflanged male relatives; and (2) the ''female choice'' hypothesis, which asserts that flanged males tolerate unflanged males in their range because they rely on female preference to favor flanged males. We investigated these hypotheses and a third hypothesis that the two male morphs represent co-existing alternative male reproductive strategies (''sitting, calling, and waiting'' for flanged males versus ''going, searching, and finding'' for unflanged males). Fecal samples were collected from a well-studied population in Indonesia, and eight human microsatellites were analyzed for 30 individuals that have been behaviorally monitored for up to 27 years. By carrying out paternity analysis on 11 offspring born over 15 years, we found that unflanged males fathered about half (6) of the offspring. Relatedness between successful unflanged males and resident dominant males was significantly lower than 0.5, and for some unflanged/flanged male pairs, relatedness values were negative, indicating that unflanged males are not offspring of the flanged males. *Key words:* fecal analysis, mating strategies, microsatellites, non-invasive sampling, orang-utans, paternity, relatedness, *Pongo pygmaeus abelii*. *[Behav Ecol 13:643–652 (2002)]*

The causes and consequences of secondary sexual characters (SSCs) for male reproductive success in vertebrates have been a dominant and controversial issue in evolutionary ecology over the last 20 years (Andersson, 1982; Jones et al., 1998; Møller, 1992). Crucial to exploring competing hypotheses as determinants of male lifetime reproductive success has been the impact of molecular ecological studies that allow an individual's genetic output to be directly measured (Jennions and Petrie, 2000; Pemberton et al., 1992). Although such studies have been applied successfully in wild primates (e.g., Altmann et al., 1996; de Ruiter et al., 1994), they have yet to be successfully applied in great apes, where special problems include logistical difficulties in sampling, long generation time, and the threatened status of many populations pertain (but see Constable et al., 2001; Gagneux et al., 1999; Gerloff et al., 1999).

Orang-utans are semisolitary, but their ranges overlap to a large extent, and they may aggregate occasionally in large fig or fruit patches (MacKinnon, 1974; Rijksen, 1978; Schürmann and van Hooff, 1986). Sometimes, in the fruiting season, these aggregations develop into bands (Sugardjito et al., 1987; Utami et al., 1997) in which individuals may travel together in a coordinated fashion. The only other time adult orang-utans associate is during reproductive consortship, when a male and female may range together for several days, weeks, or even months and engage in sexual behavior (Rijksen, 1978). Other individuals (females, unflanged males, and adolescents) may also congregate around consorting individuals (Schürmann and van Hooff, 1986), although fully mature, flanged males never associate and usually behave antagonistically toward each other (e.g., Mitani, 1985a; Rijksen, 1978; Rodman and Mitani, 1987).

Orang-utans exhibit extreme sexual dimorphism in male SSCs such as flanged cheeks and a throat sac, which enables them to produce loud calls to advertise their presence (Galdikas, 1985b; MacKinnon, 1974; Rijksen, 1978; Rodman, 1984). These characteristics are hypothesized to have arisen as a result of sexual selection in which female choice or male–male competition has played an important role (Rodman and Mitani, 1987; Schürmann and van Hooff, 1986). In addition, there is remarkable bimaturism among adult males, who vary considerably in the age at which their SSCs develop. In some males this transition may be delayed until around the age of 30 (see below). Although these unflanged or ''arrested'' males lack SSCs, they are fertile, sexually active, and can sire offspring (Kingsley, 1982; Maggioncalda, 1995). Social factors, such as the presence of a dominant adult male, are thought to influence the delay of SSC development in such males (Maggioncalda, 1999; Schürmann and van Hooff, 1986).

Bimaturism has been studied in apes by Leigh (1995) and Leigh and Shea (1995), who attributed adult dimorphism in orang-utans to sexual selection for indeterminate male

growth. To date, the most comprehensive study that has found evidence, from both behavioral and genetic data, of a clear-cut relationship among male secondary sexual development, social dominance, copulatory behavior, and reproductive success was carried out in mandrills (*Mandrillus sphinx*; Wickings et al., 1993). The authors identified two morphological variants of adult male; ''fatted'' males (with maximum secondary sexual coloration and which occupy dominant positions in the social group) and ''non-fatted'' males (with muted secondary sexual adornments, smaller testes, and which live as peripheral/solitary individuals). DNA fingerprinting analyses showed that only the two most dominant fatted males in the group fathered offspring. Male rank and mating success were strongly correlated and the alpha male sired 80–100% of the resulting offspring during 3 consecutive years.

Flanged and unflanged males also differ in their mating strategies. Flanged males, and especially dominant individuals, often establish consortships with potentially reproductive females and are usually preferred by females (Utami, 2000). Unflanged males engage in consortships comparatively rarely, but often try to copulate with females, even when they resist (Galdikas, 1985b; MacKinnon, 1974; Mitani, 1985a; Rijksen, 1978; Schürmann and van Hooff, 1986). Two hypotheses have been put forward to explain these mating patterns and to understand how two different adult male morphs can co-exist in an evolutionarily stable situation and here we posit a supplementary hypothesis related to the second.

The range-guardian hypothesis

The range-guardian hypothesis asserts that flanged males are postreproductive and defend a range in which they tolerate sexually active, unflanged males who are related to them. MacKinnon (1974) first reported sexual interactions among orang-utans. However, he never observed sexual behavior by a flanged male, but repeatedly observed both forced and unforced matings by unflanged males. A model where flanged males are postreproductive and defend a range in which they tolerate sexually active, unflanged males is only sustainable in an inclusive fitness context (e.g., if flanged males selectively tolerate sons or other male relatives). However, a number of more recent studies have shown that flanged males can be sexually active, mostly while engaged in a consortship (Mitani, 1985a; Schürmann, 1982; Schürmann and van Hooff, 1986). Therefore, a model implying a totally nonreproductive role for flanged males is questionable. However, selective tolerance of unflanged male relatives based on inclusive fitness benefits cannot be rejected based on these observations. The evolutionary predictions of this hypothesis are that unflanged males have a share in reproduction and that flanged and unflanged males in an overlapping range are related.

The female choice hypothesis

The female choice hypothesis asserts that flanged males tolerate unflanged males in their range because they rely on female preference to favor flanged males. Schürmann and van Hooff (1986) and van Hooff (1995) have argued that the co-existence of two sexually mature male morphs could only have evolved as stable alternative strategies if it is assumed that female choice plays a pivotal role. This contrasts with the view of Rodman and Mitani (1987), who proposed that the extreme sexual dimorphism of orang-utans and their bimaturism rests solely on strong male–male competition and that female choice plays no role in the evolution of bimaturism. However, because fertile female orang-utans are usually widely dispersed spatially (Galdikas, 1985b; Rijksen, 1978; Rodman and Mitani, 1987; Schürmann and van Hooff, 1986; van

Schaik and van Hooff, 1996), and given the dense character of the forest habitat and the large size of orang-utan home ranges, it is difficult to envisage how a dominant flanged male could permanently control access to all the females in his range (van Hooff and van Schaik, 1992). Thus, other males might still have the opportunity to gain access to females, especially unflanged males who are less conspicuous and do not advertise their presence. Moreover, it would seem evolutionary feasible for flanged males to invest in growth and in defending a territory against other flanged males, while tolerating unflanged males to some extent, if females had a preference for flanged males when it really mattered (i.e., when they are fertile; van Hooff, 1995). Consequently, the prediction would be that flanged males fertilize the females.

The sit-and-wait versus go-and-search hypothesis

The sit-and-wait versus go-and-search hypothesis asserts that flanged males and unflanged males represent alternative reproductive strategies. This hypothesis (a variant to the female choice hypothesis) posits that unflanged males are also reproductively successful because the two male reproductive strategies are at an evolutionary stable equilibrium. Flanged males are reproductively successful because they are preferred by females in most cases. Flanged males sit and wait for fertile females that are attracted by their long calls and subsequently consort with them. Flanged males would have to tolerate unflanged males because of the difficulty of excluding them effectively. This allows unflanged males to go and search for females in a less conspicuous and therefore less provocative manner. Under this scenario it could be possible that the presence of unflanged males would attract more females, as has been suggested for satellite males who are tolerated by male lek winners in the ruff *Philomachus pugnax* (van Rhijn, 1973). The prediction would be relatively low reproductive success for unflanged males, as has been observed in a recent study of reproductive success in ruff (Burke T, personal communication) and in Bullock's orioles, which demonstrate age-specific plumage characteristics (Richardson and Burke, 1999).

Microsatellites are now used routinely in primates for paternity and relatedness analyses (Altmann et al., 1996; Gagneux et al., 1999; Gerloff et al., 1999; Keane et al., 1997; Morin et al., 1994; Nievergelt et al., 2000), and many human-derived microsatellite loci have been described as suitable in a large number of primates (e.g., Coote and Bruford, 1996), especially in the apes (e.g., Clifford et al., 1999; Field et al., 1998; Goossens et al., 2000b). Recent technical developments in the use of noninvasively collected samples (Taberlet et al., 1999) such as hair (e.g., Gagneux et al., 1999) and feces (e.g., Kohn and Wayne, 1997) now provide the possibility of studying endangered species such as orang-utans.

To test the hypotheses described above, we compared mating pattern data collected during a 30-year field study in Ketambe, Gunung Leuser, Sumatra, Indonesia, with genetic data derived from polymorphic human-derived microsatellites and DNA extracted from fecal samples.

METHODS

Behavioral observations

The study was carried out at the Ketambe Research Station, Gunung Leuser National Park, southeast Aceh, northern Sumatra, Indonesia. The site is approximately 450 ha large and is bordered on two sides by the Alas River and the Ketambe River. The area mainly consists of undisturbed, primary lowland rainforest (Rijksen, 1978; van Schaik and Mirmanto, 1985). Orang-utans have been studied at Ketambe since 1971
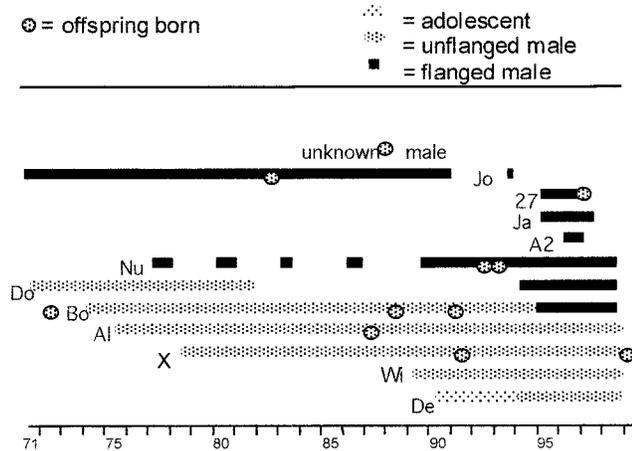
Figure 1
Summary of reproductive careers for unflanged and flanged males in Ketambe. The x-axis represents the year. Breaks in lines represent periods when the males disappeared from the study site. Two-letter descriptors of male names correspond to Table 2, except for Bobby, who is here described as ''27.''

(Rijksen, 1978) and were habituated by previous researchers. They are recognized individually, and the life history of most animals has been well documented.

Most of the behavioral data were collected between January 1993 and October 1995 and consist of 8918 h of focal animal sampling (Altmann, 1974). In addition, data from previous studies on this same population have been used (Rijksen, 1978; Schürmann, 1982; Schürmann and van Hooff, 1986; te Boekhorst et al., 1990; Utami and Mitrasetia, 1995; Utami et al., 1997) and cover 11 adult males who were observed to have been in contact with females. Different individuals were followed simultaneously where possible by different observers, and observation methods were standardized.

We distinguished the following categories of flanged males: resident males (seen regularly in the area, but not always as a dominant); dominant males (were able to displace all other males in the area and were usually, but not necessarily, resident); and nonresident males. The dominance status was determined on the basis of interactions between males. Interactions can be agonistic (avoidance, threat, chase, and fighting) and nonagonistic (Utami et al., 1997). The status of the males (unflanged and flanged) which were not excluded and their sexual contacts with the females in our population are described in detail in Utami (2000). Figure 1 presents a summary of male careers and offspring sired.

We defined copulations as interactions between males and females that included at least one intromission. Forced copulations were initiated by a male and resisted by struggling, biting and/or screaming. Cooperative copulations involved nonresisting females and were initiated by either the male or the female.

We assume that the reproductive status of a female most directly influenced her sexual activity as well as her preference for a specific partner. Orang-utan females do not display patterns of sexual swelling, and it is difficult to estimate time of ovulation. It is only a few weeks after conception that a pregnancy-related swelling of the labia is observed (Schürmann and van Hooff, 1986). The nearest approximation to the reproductive stage, in our case, is the presence and age of offspring. Because we know that the interbirth interval is approximately 8 years (Galdikas and Wood, 1990), we assume that from 6 years after having given birth to a surviving offspring, the females are potentially reproductively active again.

Table 1
Characteristics of the eight human microsatellites used in the study

Locus	T_a (°C)	Size (bp)	Heterozygosity		
			No. of alleles	Observed	Expected
D5S1457	45	102–118	4	0.37	0.58
D5S1470	45	191–219	7	0.83	0.78
D3S1766	50	203–223	5	0.73	0.64
D2S141	47	145–161	8	0.70	0.66
D17S791	47	148–170	7	0.66	0.62
D12S375	52	164–184	6	0.72	0.73
D4S243	47	172–188	5	0.56	0.73
D1S550	47	133–157	5	0.69	0.73

All primers are available from Research Genetics as Human Map-Pairs™. T_a is the optimal PCR annealing temperature.

Sampling

Forty individuals were observed in Ketambe between 1972 and 1998: 16 males, 9 females, and 15 offspring. Between 1993 and 1998, a total of 90 fecal samples were collected for 11 males (69% of those observed during this period), 6 adult females (67%), and 11 offspring (73%), shortly after defecation. The samples were stored in 90% ethanol. Precautions were taken to avoid human contamination by using sterile gloves and implements.

DNA extraction

Fecal extractions were carried out in a class I microbiological safety hood, using the QIAamp DNA Stool Mini Kit provided by Qiagen GMBH (Hilden, Germany, catalogue no. 51504; Goossens et al., 2000a). For each fecal sample, three DNA extractions were carried out. The protocol is described in Goossens et al. (2000a).

Microsatellite analysis

Eight human microsatellite loci tested on blood and tissue samples from captive orangutans (Zoological Society of London Blood and Tissue Bank) were used and shown to be polymorphic: two dinucleotide loci D2S141 and D17S791, and six tetranucleotide loci D1S550, D3S1766, D4S243, D5S1457, D5S1470 and D12S375 (Table 1; see also Coote and Bruford, 1996; Gerloff et al., 1999; Goossens et al., 2000b; Launhardt et al., 1998). All forward primers were fluorescently labeled. All polymerase chain reactions (PCRs) were carried out in a total volume of 12.5 μl reaction mix containing 2.5 μl DNA extract. We conducted a multiple-tube procedure for each fecal extract according to Taberlet et al. (1996; see also Constable et al., 2001; Gerloff et al., 1999; Kohn et al., 1999; Launhardt et al., 1998). For each extract and each locus, three amplifications were performed (Goossens et al., 2000a). After that, the most successful extract (three positive PCRs) for each sample was reamplified seven times to confirm genotypes and avoid typing errors (see Taberlet et al., 1999, for a review), even if three heterozygotes were obtained after three PCRs. This procedure gives a 99% genotype confidence level (10 independent PCRs; Taberlet et al., 1996). Amplifications were carried out in a solution of 12.5 μl 10 mM Tris-HCl (pH 9.0), 200 mM $(NH_4)_2SO_4$, 50 μM each dNTP, 1.5 mM $MgCl_2$, 5 ng of bovine serum albumin, 0.1 U Amplitaq® Gold DNA polymerase (Perkin Elmer), 0.5 μM nonfluorescent reverse primer, 0.5 μM fluorescent (TET, FAM or HEX) forward primer, and 2.5 μl of DNA extract. A PCR amplification of 50 cycles

Table 2

Paternity of 11 offspring born in Ketambe study site

Offspring (year of birth)	Mother r (cub–mother)	Males				
		Dedi	Wiba	X	Aldo	Boris
Ans (1975)	Binjei	5	5	4	2	0
	0.531	−0.747	−2.320	−1.490	1.520	2.420
						0.992
						0.552
Chris (1987)	Ans	2	4	3	0	1
	0.793	0.163	−1.420	1.860	3.240	0.625
					0.932	0.712
					0.758	0.531
Yossa (1992)	Yet	1	2	3	3	1
	0.371	1.440	−0.533	−0.383	−1.350	1.590
		0.996				0.996
		0.279				0.270
Peter (1983)	Pluis	4	4	2	5	3
	0.672	−2.220	0.415	0.342	−3.140	−1.630
Eibert (1991)	Elisa	2	5	1	1	0
	0.844	0.079	−1.870	−0.740	0.814	0.534
				0.561	0.561	0.561
				−0.127	−0.127	0.395
Setia (1993)	Sina	1	4	2	2	2
	0.710	1.030	−0.663	0.028	−0.263	−0.256
		0.971				
		0.592				
Herman (1988)	Getti	1	3	3	1	0
	0.716	0.085	−0.816	−1.450	1.370	0.570
		0.882			0.972	0.882
		0.109			0.281	0.219
Tati (1988)	Binjei	5	4	4	2	4
	0.372	−1.510	−0.554	−0.788	0.214	0.162
Puji (1991)	Pluis	3	3	0	3	3
	0.769	−1.700	1.050	1.470	−2.620	−2.100
				0.945		
				0.347		
Gendhuk (1997)	Getti	4	3	5	3	4
	0.463	−0.479	−0.269	−1.610	−1.990	−0.902
Kelly (1996)	Ans	1	3	0	4	3
	0.507	−0.215	−0.426	1.390	−1.740	0.582
		0.931		0.931		
		0.103		0.356		
r with Jon[c]		−0.438**	0.001**	0.223*	−0.160***	−0.177**
r with Nur		0.285	0.116*	0.161	−0.085**	−0.032*

All males are potential fathers. F indicates flanged males. The two values for each male indicate number of loci by which the male is excluded (top; 0 indicates the father), and log likelihood inference of paternity (LOD score, bottom). The third and fourth values tiled for some males (non-excluded or excluded by only one locus) are the exclusion probability and the relatedness values, respectively.

[a] Behavioral data indicate the flanged male that was the dominant/resident (Dom/res) male at the time of the offspring conceptions (the u indicates unstable period of adult male rank) as well as observed consortships between the mother and the flanged or unflanged male at the time of conception of some offspring.

[b] Boris was a resident unflanged male since 1973 and became a resident flanged male in January 1993.

[c] Relatedness values (r) are indicated between the two dominant/resident flanged males Jon and Nur and the unflanged males, asterisks indicate that this value significantly differs from $r = 0.5$ (* $p < .05$, ** $p < .01$, *** $p < .001$); none of the values significantly differed from unrelated ($r = 0$).

was carried out (initial denaturation 94°C for 10 min, 94°C for 15 s, 45°C to 52°C for 15 to 30 s, 72°C for 30–60 s). The annealing temperature was optimized for each locus (Table 1). All PCR products were separated on an acrylamide gel using an ABI PRISM 377 DNA sequencer. We analyzed gels using GeneScan Analysis 2.0 and Genotyper 1.1 software.

Data analysis

We analyzed paternity in two different ways. First, using the exclusion method, potential fathers (males that were present in the study area during the period of conception and from whom a genetic sample was obtained) were excluded if they

Table 2, extended

Males						Behavioral data[a]	
Doba (F)	Nur (F)	A2 (F)	Jan (F)	Bobby (27) (F)	Jon (F)	Dom/res flanged male	Observed consortships
3 −1.150	4 −0.931	3 0.249	3 −0.091	4 0.073	3 −0.124	Jon	Jon, Boris
3 −1.300	3 −1.120	3 0.462	3 −0.130	5 −1.500	3 −0.581	Jon, Erik (u)	
2 0.474	0 1.340 0.907 0.639	4 −1.090	3 −0.210	4 −1.860	3 −0.855	Nur	Nur
3 0.275	2 −0.060	4 −0.323	4 −0.626	2 1.13	0 1.560 0.971 0.764	Jon	Jon
2 −0.877	2 −0.054	3 −0.654	3 −0.119	3 −0.327	2 0.673	Jon	
3 −1.160	0 1.430 0.954 0.711	5 −1.410	3 −0.071	3 −1.370	3 −0.234	Nur	Nur
4 −1.320	2 −0.598	4 −0.489	2 −0.173	6 −2.890	2 0.714	Jon, Erik (u)	
3 −0.707	4 −1.310	4 −0.247	5 −1.010	3 0.985	5 −1.680	Jon	
2 0.513	2 0.307	4 −0.146	3 −0.057	2 0.895	2 −0.054	Jon, Nur (u)	X
3 −1.310	2 −0.613	3 −1.370	3 −0.099	0 3.120 0.999 0.466	4 −1.020	?	
4 −1.560	1 0.161 0.860 −0.124	5 −2.420	3 −0.055	2 −0.562	2 0.820	Boris,[b] Jan (u)	X

did not possess an allele in the offspring which it could not have inherited from its mother. If all potential fathers are tested and if sufficient markers have been included, all but one male, the father, can be excluded. The probability of exclusion was calculated using the method of Chakraborty et al. (1988) and was implemented using POPASSIGN 3.8 (Funk SM, Zoological Society of London).

The second paternity assessment method was inclusion. For this analysis, we used the program CERVUS 1.0 (Marshall et al., 1998), which was also used to assess the possible occurrence of null (nonamplifying) alleles that could result in false paternal discrepancies. This program identifies the most likely father from a panel of potential fathers by correlating the genotypes of the males to the most likely genotype of the father (see, e.g., Coltman et al., 1998; Constable et al., 2001; Gerloff et al., 1999; Kohn et al., 1999; Nesje et al., 2000; Rossiter et al., 2000). With this method a potential father can also be implicated if not all potential fathers have been sampled or if the number of loci is not sufficient to exclude all males who are not the father. We assessed males that were candidates for paternity of each offspring from frequency of sightings during the period when each offspring was conceived and averaged six males per offspring. Estimations from field observations suggest that approximately 70% of males were sampled. The proportion of loci typed (0.95) and the loci mistyped (0.01) are average values across eight loci. We estimated the rate of typing error from mother–offspring mismatches. Paternities were assigned using CERVUS 1.0 at levels of 95% confidence, and 10,000 paternity simulations were generated.

Relatedness between flanged males and unflanged males living in the same area were calculated using the program Kinship 1.3 (Queller and Goodnight, 1989). Relatedness values may vary from +1 (identical twins) through 0 (average

relatedness in the population) to −1 (originating from another gene pool). We tested the hypothesis that the unflanged males were unrelated to the flanged male by comparing their relatedness against the hypothesis that the unflanged males were sons of the flanged males ($r = 0.5$). We also calculated relatedness between non-excluded father–offspring, one-locus–excluded father–offspring, mother–offspring, father–mother, all mature males, adult females, and all individuals.

RESULTS

Genetic analysis

We genotyped 11 potential mother–offspring pairs and 11 potential fathers. The number of alleles per locus ranged from 4 (D5S1457) to 8 (D2S141), and expected heterozygosities ranged from a minimum of 0.58 (D5S1457) to a maximum of 0.78 (D5S1470; Table 1). The estimated frequency of null alleles was 0.021. Allelic dropout and false alleles (Taberlet et al., 1996, 1999) were identified in two individuals, and additional PCRs on two other extracts were performed to assess the true genotype for a heterozygous individual. Homozygous individuals for a locus were assessed only if seven independent PCRs detected the same allele for a particular extract. All 11 offspring analyzed contained fully compatible multilocus genotypes with their known mother.

The results are summarized in Table 2. Each offspring is compared with each male in terms of the number of loci at which the male is excluded, and the paternal exclusion probability is given for the non-excluded father and the one-locus–excluded males. The log likelihood inference (LOD score) of paternity is also given in Table 2. The LOD score value is the highest for 7 of the 10 included fathers. We found the following mean pairwise relatedness estimates and standard errors: mother–offspring, 0.613 ± 0.051; father–offspring, 0.521 ± 0.061; one-locus–excluded father–offspring, 0.221 ± 0.072; included father–mother, 0.080 ± 0.081; all potential fathers, −0.09 5 ± 0.081; all males (flanged and unflanged), −0.091 ± 0.030; adult females, −0.108 ± 0.070. Relatedness values between the two dominant/resident flanged males "Jon" and "Nur" and the unflanged males are also indicated in Table 2.

Paternity and relatedness

Paternity analysis implicated a single male in 10 out of 11 cases. In six of these cases an unflanged male was implicated as the father, and in four cases a flanged male was implicated. Of the seven cases where consorting males were observed, in four cases the consorting male was indicated as the father, and in three out of these four cases the father was an unflanged male (see behavioral data in Table 2). It was not possible to include all males that might have had sexual interactions with the females (some males who were present at the time of the conceptions were no longer present at the time of genetic sampling and, moreover, females may have ranged outside of the monitored area and mated with unknown males). Jon was the resident/dominant flanged male at the time of the conception for four of the sampled offspring. However, he was excluded as father for three of the offspring by at least two loci. Of the 11 potential fathers in our study, three were flanged males, and two of these fathered offspring during their tenure (Jon dominant > 15 years; Nur dominant < 5 years). In the four cases of conception that occurred when the male dominance relationships appeared to be unstable, unflanged males fathered all offspring.

In Table 2, the Queller-Goodnight relatedness values are given between the two dominant/resident flanged males Jon and Nur and the unflanged males. Relatedness between Jon and all the unflanged males found in the study area and between Nur and Aldo (flanged and unflanged males, respectively, from the same territory) were significantly lower than 0.5; and for some unflanged/flanged male pairs, relatedness values were strongly negative (Jon/Aldo, $r = -0.160$; Jon/Boris, $r = -0.177$; Boris/X, $r = -0.292$). None of the values were significantly different from unrelated ($r = 0$; Table 2). Mean relatedness values for all adult males (−0.095) and all adult females (−0.108) are negative, showing that both adult males and adult females are mostly unrelated in our population.

DISCUSSION

Six out of 10 tested offspring could be attributed to three of the unflanged males and just four offspring to three flanged males. How do these results correspond to the predictions of the three hypotheses?

First, the hypothesis that resident flanged males are postreproductive guardians of a territory inhabited by male relatives can be rejected because flanged males are the most likely fathers of about half of the offspring. Furthermore, the relatedness between the flanged males and the unflanged males present in the area at the time of conception of the offspring does not support this hypothesis. Boris, an unflanged male, fathered three offspring during Jon's tenure (a flanged male). The estimated relatedness value between Jon and Boris was −0.177, a value significantly lower than 0.5, but not significantly different from 0. Thus we may conclude that Jon and Boris are not closely related. The range-guardian hypothesis also implies that males must be comparatively philopatric, or, when migrating between habitats, that certain unflanged males migrate in coordination with an adult male (van Hooff, 1995). The mean pairwise relatedness values for all adult males (−0.091 ± 0.030) and for all adult females (−0.108 ± 0.070) suggest that females may be more unrelated than males are, although the difference is not significant. This finding does not support the hypothesis that maturing females tend to remain in their natal area, whereas males disperse (Rodman, 1973). These relatedness values for both sexes do, however, reflect records for Ketambe that suggest dispersal by both sexes.

Second, the female choice model in which fertile females have an exclusive preference for flanged males, and therefore unflanged males never father offspring, can also be refuted. The finding that unflanged males are responsible for about half of the tested offspring shows that flanged males do not have a reproductive monopoly. The female choice model cannot be maintained in its most strict form; however, the role of female choice cannot be rejected. This model was based on the consideration that a dominant flanged male could never fully control access to the females, given the large size of home ranges, the dense character of the forest habitat, and the cryptic fertility of females. Thus, other males would still have an opportunity to gain access to a female. This applies particularly to unflanged males, who refrain from making their whereabouts known by producing long calls (Mitani, 1985b) and who are able to roam, often without provoking aggression from flanged males. However, if females did not exert a preference for flanged males, it would be difficult to see how flanged males could obtain the reproductive advantage required to maintain such costly traits.

Alternative male mating strategies have been demonstrated for mammals, birds, and fish. In Antarctic fur seals (*Arctocephalus gazella*), holding a land-based territory was expected to confer a reproductive advantage to males. However, a recent study has shown that at least 70% of the pups born in the study site in a given year are not fathered by males who held

a territory or were observed copulating with females in the previous year (Gemmell et al., 2001). This implies that a pool of males exists that seldom venture ashore at this site. The authors suggested that female choice is an integral component of the Antarctic fur seal mating system and that aquatic mating may be an alternative mating strategy in this species.

In the ruff, two different adult male morphs coexist (van Rhijn, 1983). Hugie and Lank (1997) have presented a model in which female choice favors the evolution and maintenance of alternative mating strategies. Resident males establish and defend courts on leks against other residents, while nonterritorial satellite males move between leks and among courts on a lek. The analysis suggested that the resident–satellite relationship is fundamentally a cooperative association favored by female choice, and in this polyandrous system territorial males have been shown to gain the majority of paternities (Burke T, personal communication).

In the long-tailed manakin (*Chiroxiphia linearis*), Trainer and McDonald (1995) highlighted a relationship between song performance and courtship success in this lek-mating species. Teams of male manakins form cooperative partnerships consisting of a dominant alpha male and a beta male partner with a variable number of subordinate affiliates. The song performance of each male may provide information useful to females in assessing a potential mate's ability to form a cooperative, long-term partnership. The alpha male is responsible for virtually all mating, whereas the beta male assists in the courtship displays. McDonald and Potts (1994) showed that alpha and beta partners are not relatives. Long-delayed benefits to beta males are demonstrated including rare copulations, ascension to alpha status, and female lek fidelity (McDonald and Potts, 1994).

The bluegill sunfish (*Lepomis macrochirus*) shows two male alternative reproductive strategies, wherein heteromorphic males specialized for parasitism or for parental care coexist (Gross, 1991). All these examples highlight that female choice and cooperative breeding may have influenced the evolution of bimaturism or dimorphism and alternative reproductive strategies in some animal species, and still may give the opportunity for beta males to access females.

The alternative mating strategies of unflanged males may confound the effects of direct male–male competition. Peripheral, young, or subordinate males of other primate species are also known to engage in alternative mating strategies. In Japanese macaques (*Macaca fuscata fuscata*), Soltis et al. (1997) showed quantitative evidence that (1) female choice can weaken the observed effects of male–male competition, and (2) when in conflict with male–male competition, female choice can be the stronger predictor of male reproductive success. In Japanese and rhesus macaques, dominant males form long-term mating series with females, but subordinate males form short-term, sometimes furtive, mating series with females (Berard et al., 1994; Huffman, 1992; Manson, 1996).

In wild patas monkeys (*Erythrocebus patas*), direct observation showed that only 31% of matings were performed by the resident male in a multi-male situation with three subordinate males in the group. In a one-male group (harem), the tenured male accounted for all matings. Paternity discrimination by DNA typing revealed that 50% of infants were sired by outsider males in a one-male situation, and that 20% of the infants were sired by intruder males directly after following take-over of a group by a new resident male. Finally, sneaky mating by females with outsider males or subordinate males was initiated by the females (Ohsawa et al., 1993).

Gerloff et al. (1999) demonstrated that in bonobos, reproductive success is biased in favor of high-ranking males, even though these do not necessarily show the highest copulation rates, but several studies suggest the existence of alternative

male competitive tactics also in great ape species (see Smuts, 1987, for a review). In chimpanzees, alpha males monopolize estrous females through possessive behavior within groups, and non-alpha males mate opportunistically within groups and form prolonged sexual consortships away from other males (Hasegawa and Hiraiwa-Hasegawa, 1983; Tutin, 1979). However, Gagneux et al. (1997) showed that half of the infants born in a chimpanzee community were sired by males from outside the group, even though extra-community copulations had not been observed. In mountain gorillas, Robbins (1999) showed that although the dominant males in two studied groups participated in the largest proportion of matings, they did not monopolize mating behavior.

In orang-utans, behavioral observations show that females consort with flanged males and engage in cooperative copulations, especially with the dominant or resident male, whereas they often resist the forced copulations of unflanged males (Galdikas, 1985b; Schürmann and van Hooff, 1986). We observed that in the Ketambe population, reproductive females prefer flanged males. They do so especially during phases of stability in the male hierarchy (Utami, 2000). However, in this population, unlike the one studied by Galdikas (1985b), some females occasionally also choose unflanged males. During periods of male rank instability such mating became more common. During such periods, in fact, both flanged and unflanged males engaged in matings with reproductive and nonreproductive females. Matings with unflanged males were not only more common, but also they were often not resisted by females. In our results, four out of six offspring sired by unflanged males were conceived during such periods of instability in male rank when dominant males were not present (see Figure 1). It is possible that only certain unflanged males may be successful. Although numbers are necessarily small, our results suggest that all reproductively successful males except for one were residents and not part of the considerable population of "floating" males (te Boekhorst et al., 1990). This lends support to the suggestion by van Schaik and van Hooff (1996) that individual pair bonds might exist.

Recent studies suggest that male dominance is not always attractive to females and that it does not necessarily predict superior parental quality, good genes, or other forms of benefit to females (in birds such as the pheasant, the pintail duck, the house sparrow; insects such as the field cricket; amphibians such as the tiger salamander; and fish such as the sand goby and the three-spined stickleback; for a review see Qvarnström and Forsgren, 1998). When traits selected by male–male competition do not reflect overall mate quality, females are expected to use other choice criteria and might occasionally prefer subordinate males (Qvarnström and Forsgren, 1998). Thus females may engage in durable relationships with certain familiar unflanged males, possibly as an investment for when they become dominant flanged males (Schürmann and van Hooff, 1986).

Whether females find the full secondary sexual characters of flanged males more attractive is currently unknown. Utami (2000) demonstrated that relationships between males depend on the presence of potentially reproductive females, and an absolute intolerance between flanged males has been observed. This reflects the strong contest competition between flanged males for access to females (Mitani, 1985a; van Hooff and van Schaik, 1995). This is in contrast with the comparatively peaceful relationships observed between flanged and unflanged males (Utami et al., in press). This means that flanged males are unable to prevent unflanged males from contacting females, even though unflanged males appear to engage in sexual interactions with the females regularly. Such tolerance would be understandable if unflanged males were reproductively less successful, which is not the case in our

study, or if female choice for unflanged males under certain circumstances would make intolerance less effective. The genetic results and observations suggest that the unflanged phase represents a specific, alternative male strategy which is extended when a dominant flanged male is in the area (van Hooff, 1995). A similar dimorphism within males has been described for another solitary primate, the lesser bushbaby (*Galago senegalensis*). Older and heavier ''A-males'' have territories and preferential social contacts with the females living in their territories and are highly intolerant of other A-males. A-males are much more tolerant toward the lighter B-males, which roam their territories. A high-ranking B-male can quickly become an A-male once a territory becomes available (Bearder, 1987).

Seemingly in contrast to our present findings in orangutans, but in a group-living species, mandrills (*Mandrillus sphinx*), which also exhibit adult male bimaturism, Wickings et al. (1993) demonstrated, in a semi–free-ranging group, a strong relationship among adult male secondary sexual development, social dominance, and reproductive success. This result is more in accordance with other studies, such as on wild long-tailed macaques (*Macaca fascicularis*), where the high-ranking males father the majority of offspring (de Ruiter et al., 1994). It is also more in accord with a study on Sulawesi crested black macaques (*Macaca nigra*), where adult females sexually solicit high-ranking males more often than low-ranking males, but frequency of copulation is not correlated with dominance rank (Reed et al., 1997). All these studies concern social species, which live in uni- or multi-male groups. Orangutans, however, are solitary, and in that situation, two alternative strategies, maintained by frequency-dependent selection (e.g., Brockman et al., 1979), may be more feasible because monopolization of females by males is more difficult. These could be (1) a sitting, calling, and waiting strategy of flanged males who would rely on female choice in relation with their SSCs and long calls and (2) a going, searching, and finding strategy of unflanged males with low costs from aggression but higher costs of finding and persuading females (Galdikas, 1985a,b; Utami, 2000). That the going, searching, and finding strategy might be successful as an alternative is suggested by the fact that a resident unflanged male had three offspring, the first of which was conceived more than 20 years before he finally became a flanged male (see Figure 1). Some males may never reach this stage, yet may be reproductively successful.

One possible complicating factor associated with these data is that in the early 1970s Ketambe was used as a rehabilitation station. When it was determined that it was problematic to introduce rehabilitants into a healthy population, these rehabilitants were recaptured and translocated. However, two of the rehabilitants, the females Binjei and Getti, could not be recaptured. Two of the six offspring assigned to an unflanged male have an ex-rehabilitant female as a mother and two have the daughter of a rehabilitant female as a mother (Kelly and Chris). There remains, therefore, the possibility that these unexpected paternities result from unusual sexual behavior of these females. However, two offspring (Eibert and Puji) fathered by unflanged males, Boris and X, respectively, have non-rehabilitant females as mothers, Pluis and Elisa, respectively.

Finally, although the data in this study concern a population that has been studied for many years, they involve a species with extremely slow demographic dynamics, and as a result sample sizes are always likely to be small. A caveat, therefore, is that an element of demographic stochasticity may bias these data, which should be regarded as information which ultimately needs to be augmented with data from continued study and from comparable sites.

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