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Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus*)

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Abstract

Behavioural observations suggest that orang-utans are semi-solitary animals with females being philopatric and males roaming more widely in search of receptive partners, leading to the prediction that females are more closely related than males at any given site. In contrast, our study presents evidence for male and female philopatry in the orang-utan. We examined patterns of relatedness and parentage in a wild orang-utan population in Borneo using noninvasively collected DNA samples from animals observed to defecate, and microsatellite markers to assess dispersal and mating strategies. Surprisingly, resident females were equally as related to other resident females (mean $r_{xy} = 0.303$) as resident males were to other resident males (mean $r_{xy} = 0.305$). Moreover, resident females were more related to each other and to the resident males than they were to nonresident females, and resident males were more related to each other (and resident females) than they were to nonresident males. We assigned genetic mothers to 12 individuals in the population, while sires could be identified for eight. Both flanged males and unflanged males achieved paternity, similar to findings reported for Sumatran orang-utans.

Keywords: dispersal, faeces, noninvasive genetics, orang-utans, relatedness, reproductive success

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Introduction

Patterns of mating and dispersal are of major importance in determining the distribution of genetic variation in a population (Chesser 1991a, b; Chesser *et al*. 1993; van Staaden 1995; Sugg *et al*. 1996; Dobson 1998; Dieckmann *et al*. 1999; Storz 1999). Most primates and other mammals are characterized by male-biased dispersal (Greenwood 1980; Pusey & Packer 1987; but see Moore 1984; Printes & Strier 1999). Such sex-biased dispersal is generally thought to be due to the greater benefits for females that remain in their natal area and that form social relationships with closely related members of the same sex, while males benefit more from dispersing due to sex differences in the determinants of reproductive success (Wrangham 1980; Pusey & Packer 1987; Clutton-Brock 1989; Gandon 1999).

African great apes are unusual, showing either dispersal by both sexes or female-biased dispersal and cohesive social groups. Both sexes disperse in mountain gorillas (*Gorilla gorilla beringei*; Harcourt *et al*. 1976; Harcourt 1978), while female dispersal with male philopatry predominates in Western lowland gorillas (*Gorilla gorilla gorilla*; Stokes *et al*. 2003; Bradley *et al*. 2004), bonobos (*Pan paniscus*; Gerloff *et al*. 1999) and chimpanzees (*Pan troglodytes*; Gagneux *et al*. 1999). This raises the question of the significance of female-biased dispersal in the evolutionary history of great apes. Observations of dispersal in the semi-solitary orang-utan — the only extant, non-African great ape, and the most distantly related to humans — are extremely rare, but

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suggest that dispersal may be male biased. This therefore suggests that female-biased dispersal of African great apes (including humans) evolved after the separation from orang-utans (Rodman 1973; Singleton & van Schaik 2002), and perhaps concomitantly with the evolution of bisexual social groups. However, for Sumatran orang-utans (*Pongo abelii*), the only genetic study available to date suggests that dispersal occurs in both sexes (Utami *et al*. 2002). No genetic data has been available to confirm this pattern for Bornean orang-utans.

We investigated the genetic structure of a population of Bornean orang-utans (*Pongo pygmaeus*), examining both the distribution of relatedness within age/sex classes of resident and nonresident animals and patterns of paternity. Empirical estimates of relatedness allow analysis of the relationship between kinship patterns and dispersal behaviour (Banks *et al*. 2002; Coltman *et al*. 2003; Radespiel *et al*. 2003; Möller & Beheregaray 2004; Hammond *et al*. 2006). If individuals do not disperse far from their natal site, those living in close proximity should be more related, on average, than the individuals randomly sampled from the whole population. We used DNA extracted from noninvasively collected faecal samples from 32 animals that were observed to defecate in a 4-km^2 study site within the Lower Kinabatangan Wildlife Sanctuary, and performed genotyping using microsatellites to test the following predictions:

1. If females are philopatric, while males disperse, relatedness between resident adult females should be higher than between resident adult males, and higher than between resident females and males.
2. If females are philopatric, then resident females should be more related to each other than they are to nonresident females (females with home ranges elsewhere or who visit the study site occasionally).
3. If both sexes disperse, resident females should be equally as related to each other as resident males. Moreover, if both sexes are philopatric, we should find high relatedness values for both classes (resident females and resident males).
4. If solitary adolescents are newly independent from their mothers, and have not yet dispersed from their natal area, then it should be possible to identify their mother in the study population.

In this study we also addressed questions relating to male reproductive strategies. While dominant reproductive males develop the cheek flanges and other secondary sexual characteristics typical of fully adult males ('flanged' males), some other reproductive males fail to develop such characteristics ('unflanged' males), remaining in an 'arrested' state of development for up to 20 years after attaining sexual maturity (Kingsley 1982; te Boekhorst *et al*. 1990; Graham & Nadler 1990; Maggioncalda *et al*. 2000). Utami *et al*. (2002) showed that both flanged and unflanged males are reproductively successful in Sumatran orang-utans (*Pongo abelii*). However, Bornean and Sumatran orang-utans have been geographically and reproductively isolated for at least 10 000 years (Courtenay *et al*. 1988), are genetically distinct (Xu & Arnason 1996; Muir *et al*. 2000; Zhang *et al*. 2001), and show differing life histories (Wich *et al*. 2004), suggesting that they may not utilise the same mating systems. We therefore examined patterns of paternity in the orang-utan population, predicting that if flanged and unflanged males adopt alternative, successful reproductive strategies, then both male morphs should have offspring in the study population.

Materials and methods

Study site and noninvasive sampling

Behavioural and ecological studies have been carried out by the Kinabatangan Orang-utan Conservation project (KOCP) on wild orang-utans in the Lower Kinabatangan Wildlife Sanctuary (LKWS), Sabah, Malaysia, since 1998. The KOCP core study area (about 4 km^2) was established in Lot 2 of the LKWS in 1998 (118°17′E to 118°18′40″E, 5°32′20″N to 5°33′30″N, Fig. 1; see fig. 1 in Ancrenaz *et al*. 2004b and Goossens *et al*. 2005 for a map of the whole LKWS). A larger extension to this core area was further developed in 2001–2002 (this area is called the extension study area and covers about 6 km^2). The entire study site (core study area and its extension) is bordered with the

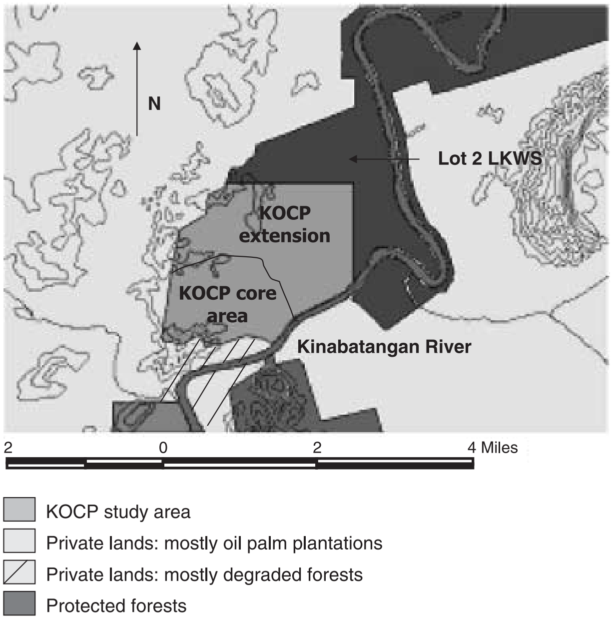

Fig. 1 Map of part of the Lower Kinabatangan Wildlife Sanctuary and location of KOCP study site in Lot 2 (see also fig. 1 in Ancrenaz *et al*. 2004b and Goossens *et al*. 2005).

Table 1 Individuals sampled in the KOCP core study area with sex, age and status [for males, flanged (fl) or unflanged (unfl)]

	Sex	Status
Resident in the core area		
SsL2.5 (+ offspring, SsL2.33)	female	adult
SsL2.36 (+ offspring, I22)	female	adult
I23	female	adult
SsL2.3	male	adult (fl)
I15	male	adult (fl)
I19	male	adult (fl)
SsL2.4	male	adult (unfl)
SsL2.10	male	adult (unfl)
Nonresident in the core area		
SsL2.20 + offspring (SsL2.2)	female	adult
I1 + offspring (I2)	female	adult
Ss8 (+ offspring, Ss9)	female	adult
I5	female	adult
I26	female	adult
SsL2.9	female	adult
Ss5	female	adult
Ss10	female	adult
I8	female	adult
I24	female	adolescent
I25	female	adolescent
Ss12	male	adult (fl)
I4	male	adult (fl)
I16	male	adult (fl)
Ss2	male	adult (unfl)
Ss7	male	adult (unfl)
SsL2.37	male	adult (unfl)
I17	male	adolescent
Ss13	male	adolescent

Kinabatangan River on its southern side, oil palm plantations on the northern side, and forests of Lot 2 of the LKWS on the eastern side (see Fig. 1). It is composed of secondary mixed lowland dipterocarp and fresh water swamp forest (Ancrenaz *et al*. 2004a). Intensive behavioural observations of wild orang-utans are conducted within the core study area only. The extension study area is patrolled by KOCP researchers to conduct regular orang-utan nest surveys and for botanical monitoring. Between April 2000 and August 2002, a total of 65 fresh faecal samples were collected within the core study area. They originated from 17 orang-utans that were individually identified as part of an ongoing behavioural study, and from 15 rarely-seen or unidentified individuals (Table 1). In all cases except two (samples Ss3 and Ss11), defecation was observed and the samples were taken immediately. Samples were stored in 90% ethanol, and sterile gloves and implements were used to avoid contamination with human DNA or cross-contamination between samples. In accordance with te Boekhorst *et al*. (1990), we calculated the monthly presence index for all orang-utans within the core study area over a five-year period (1998–2002) and distinguished between resident and nonresident individuals. Resident individuals were regularly seen within the core study area and most of their range was overlapping with it (KOCP, unpublished data). Nonresident animals were seen infrequently within the core area, but part of their range included the core as well as the extension study areas (see also MacKinnon 1974; Delgado & van Schaik 2000; Singleton & van Schaik 2001).

Although we can be sure that unflanged males were unflanged prior to the beginning of long-term behavioural observations at KOCP in 1998 (the change from unflanged to flanged status is irreversible; van Hooff & Utami 2004), we did not know how long males that were already fully flanged at the beginning of the study had had this status. Our sample of potential offspring for flanged males was thus limited to offspring born since behavioural observations began ($n = 5$ offspring).

Unbiased relatedness analysis requires that allele frequency distributions stem from unrelated individuals from the same population, but other than the target individuals for whom pairwise relatedness is estimated. We therefore used a total of 95 individuals from the same riverside as the KOCP study site, including Lots 2, 4, 5, 7, 8 and 10 of the LKWS (see fig. 1 in Goossens *et al*. 2005). Note that we have recently shown that genetic differentiation is very limited between lots from the same riverside (Goossens *et al*. 2005).

DNA extraction and microsatellite genotyping

DNA was extracted and microsatellites amplified, electrophoresed and analysed exactly as in Goossens *et al*. (2005), except that only 13 of the 14 previously described microsatellites were analysed (this was due to technical problems encountered with locus D16S420). We also conducted exactly the same multiple-tube procedure for each faecal extract as in Goossens *et al*. (2005).

Data analysis

Consistency of genotypes obtained from faecal samples was verified using the criteria set out by Taberlet *et al*. (1999), and inconsistent genotypes were excluded. GENEPOP version 3.3 (Raymond & Rousset 1995) was used to calculate F_{IS} values according to Weir & Cockerham (1984), and deviation from Hardy–Weinberg equilibrium using the exact probability test. POPASSIGN (Goossens *et al*. 2002; available at www.darwinfox.org), was used to calculate allelic diversity A, observed heterozygosity H_O, and expected heterozygosity H_E, probabilities of identity (PI and PI_{sib}, Waits *et al*. 2001) and to identify faecal samples that were identical over all 13 loci. Faecal samples providing identical genotypes to ones already sampled were excluded from the data set.

Popassign was also used to estimate within- and between-group relatedness using Queller & Goodnight's (1989) estimator, r_{xy}. Because of nonindependence of pairwise r_{xy} values, we estimated standard deviations by jackknifing over loci. Jackknifing over loci characterizes the amount of variation due to differences among loci. We also reported standard deviations of r_{xy} estimates, which better reflect the variation of r_{xy} between pairs of individuals. Relatedness analysis was performed for individuals within the KOCP study area using allele frequency distributions of individuals outside the main study population. We also used the program relatedness 5.0.8 (Goodnight & Queller 1999) to verify pairwise relatedness estimates. Both programs produced identical results.

Precision and standard deviation of r_{xy} was assessed by rarefaction analysis (e.g. Girman *et al*. 1997) using 10 000 simulated dyads, and by relatedness and kinship analysis of dyads with known (mother–offspring) or inferred (father–offspring, sibs) kinship, using popassign. First, dyads of parent–offspring were simulated with relatedness (r_{xy}) of 0.5. Loci were then selected in random order and r_{xy} was estimated for incrementally increasing numbers of loci, l, for the simulated dyads. We then examined the difference between consecutive $r_{xy,l}$ values as a function of the number of loci. Pairwise relatedness estimates r_{xy} are statistically nonindependent from each other and require permutation re-sampling for statistical comparisons (e.g. Coulon *et al*. 2006). To compare mean relatedness between two groups of individuals we conducted 1000 random resamplings without replacement, keeping sample size in each group constant. The difference between mean r_{xy} values in resampled sets was compared with the observed mean between the two groups. We considered the difference to be significant at the 5% level when the observed difference in absolute average relatedness exceeded 95% of the values obtained by permutations.

Maternity and paternity were assigned for animals conceived in or after 1985 using the programmes popassign and cervus 2.0 (Marshall *et al*. 1998). Candidate mothers and fathers were identified in popassign by age, excluding nonmature individuals as candidate parents. In the wild, females reach sexual maturity between 11 and 15 years of age and first breeding may not occur until several years later (Delgado & van Schaik 2000). Males reach sexual maturity at about 8 to 10 years in captivity, and probably later in the wild (Delgado & van Schaik 2000). The exclusionary power across all loci used for one-parent and second-parent scenarios was estimated according to Jamieson & Taylor (1997). For maternity analysis, only resident and nonresident females from the KOCP study site were considered. For paternity analysis, all males from KOCP study site and the surrounding forest, Lot 2 of the LKWS, were considered. Cervus generated the likelihood ratio (LOD) of the most likely vs. the second most likely parent based on the number of candidate parents, the proportion of candidate parents sampled, the observed allele frequency distributions, the relatedness between candidate parents and the estimated genotyping error. We used 10 000 simulations, a strict confidence level of 0.95 and a relaxed confidence level of 0.80 and allowed for relatedness between candidate parents. We estimated the genotyping error, the proportion of candidate parents sampled and the overall relatedness between candidate parents from the data. Popassign implements parentage exclusion analysis, estimates pairwise relatedness r_{xy} according to Queller & Goodnight (1989) and tests the kinship hypothesis of a parent–offspring relationship vs. the alternative hypothesis of half-sibling relationships (Goodnight & Queller 1999). We assigned mothers and fathers independently for the approaches of combined exclusion/kinship analysis and the cervus analysis. The combined exclusion/kinship analysis assigned parentage by one of three hierarchical criteria: (i) only one candidate was identified and had no exclusions with the offspring tested; (ii) several candidates had no exclusions, but only one candidate had a significant kinship relationship of parent–offspring; and (iii) several candidates had no exclusions, but only one candidate mother together with one candidate father had no pair exclusions. The criterion used for accepting mothers and fathers according to the maximum-likelihood analysis in cervus was significance at the 80% level. Mothers and fathers were finally accepted when both analyses identified the same individuals or by maximum-likelihood analysis in cases where no mother/father could be identified by exclusionary analysis.

Results

Reliable genotypes were obtained for 44 (68%) of 65 faecal samples collected within the core study area. Thirty-four different multilocus genotypes (individuals) were identified, including genotypes for the 32 known individuals (see Materials and methods, Table 1), and for two that were completely unknown (Ss3 and Ss11), and were therefore of unknown sex, age and status. In our analysis, we included a total of 23 adult individuals (12 females and 11 males), while the other animals were dependent infants and adolescents. Out of the 23 adults, eight individuals (five adult males, three adult females) were residents of the core study area.

Consistency of the genotypes was checked using the criteria set out by Taberlet *et al*. (1999): 33 individuals had reliable genotypes for all 13 loci, and one individual had reliable genotypes for 10 out of 13 loci. For the 95 additional individuals genotyped, all individuals except two (12/13) had reliable genotypes for all loci. Five genotypes (0.30%) were therefore coded as missing genotypes in the analysis.

Table 2 Number of genotyped individuals *n*, allelic diversity *A*, observed heterozygosity H_O, expected heterozygosity H_E, and F_{IS} (Weir & Cockerham 1984) for the main and extended KOCP study site. F_{IS} values were calculated for adults only

	Riverside 2 (including KOCP study site)					KOCP study site									
Locus	#ind.	Percentage scored	*A*	H_O	H_E	# ind.	Percentage scored	*A*	H_O	H_E	F_{IS} ($n = 33$)	F_{IS} flanged males ($n = 5$)	F_{IS} unflanged males ($n = 4$)	F_{IS} non resident females ($n = 9$)	F_{IS} flanged females ($n = 3$)
D5S1457	129	100	6	0.69	0.74	34	100	4	0.76	0.63	−0.214	−0.395	−0.143	−0.29	−0.25
D5S1470	129	100	8	0.76	0.74	34	100	7	0.94	0.78	−0.204	−0.2	−0.132	−0.163	−0.02
D6S501	129	100	8	0.77	0.69	34	100	5	0.82	0.64	−0.286	−0.667	−0.471	−0.19	−0.316
D3S2459	129	99.2	6	0.72	0.76	34	97.1	6	0.88	0.78	−0.128	−0.2	0.286	−0.429	−0.136
D2S1326	129	99.2	7	0.7	0.74	34	100	7	0.91	0.75	−0.214	−0.304	−0.277	−0.277	−0.19
D4S2408	129	100	4	0.71	0.67	34	100	4	0.82	0.68	−0.221	−0.364	−0.389	−0.333	−0.471
D5S1505	129	99.2	8	0.78	0.76	34	100	4	0.82	0.65	−0.274	−0.282	−0.471	−0.277	−0.579
D4S1627	129	99.2	6	0.77	0.72	34	97.1	4	0.79	0.7	−0.13	−0.304	0.25	−0.538	−0.19
D13S321	129	100	5	0.78	0.76	34	100	4	0.79	0.66	−0.167	−0.087	−0.395	0.216	−1
D13S765	129	100	5	0.64	0.64	34	100	4	0.65	0.56	−0.149	−0.389	0.062	−0.25	−0.053
D12S375	129	100	5	0.78	0.68	34	100	5	0.79	0.69	−0.15	−0.282	−0.212	0.024	−0.22
D1S550	129	100	6	0.68	0.74	34	100	5	0.71	0.68	−0.039	−0.25	0.286	−0.087	0.118
D2S141	129	99.2	5	0.76	0.74	34	97.1	4	0.82	0.67	−0.224	−0.538	0.333	0	−0.463
mean ± SD		99.69	6.08	0.73	0.72		99.33	4.85	0.81	0.68	−0.185	−0.328	−0.098	−0.2	−0.29
		0.41	1.32	0.05	0.04		1.27	1.14	0.08	0.06	0.067	0.15	0.306	0.201	0.288

The 13 loci used showed high allelic diversity and heterozygosity in the both the KOCP study site and the whole sample (Table 2). Probabilities of identities were $PI = 3 * 10^{-11}$ and $PI_{sib} = 4 * 10^{-6}$, respectively, across all loci for the main study population. No significant deviation from Hardy–Weinberg equilibrium was detected in either the KOCP study site ($P = 0.10$, Fisher's exact test) or the whole sample ($P = 0.55$). However, there was a large excess of heterozygotes and predominantly negative F_{IS} values in the study site (Table 2). Rarefaction analysis (Girman *et al.* 1997) of all 92 individuals used to calculate base allele frequency distributions for relatedness analysis indicated that the curves of mean pairwise $r_{xy,l}$, simulated for $r = 0.5$, and the difference between consecutive $r_{xy,l}$ values as well as their standard deviations, asymptoted after eight loci (Fig. 2). Mean $r_{xy,l}$ values for eight and 13 loci were 0.490 ± 0.13 and 0.495 ± 0.10, respectively. The differences between consecutive $r_{xy,l}$ values for seven and eight loci, and for 12 and 13 loci, were 0.04 ± 0.03 and 0.02 ± 0.02, respectively. This implies that the 13 loci used here were sufficient to reliably assess relatedness.

Relatedness

Mean pairwise relatedness ± standard deviation (SD) values within demographic units in the main study are shown in Table 3, with comparisons between units. Relatively low SD values, jackknifed over loci, indicate that there is little variation across loci. However, SD of pairwise relatedness was generally large. Relatedness approximately at the level of half-sibs ($r = 0.25$) was observed among females and males resident in the core area, and between males and females in the core area. In the whole KOCP study site, relatedness was approximately half that value ($r = 0.125$) between females, between all males, between flanged and unflanged males, and between all males and females. None of the comparisons between these demographic units were significantly different from each other. All individuals resident in the core area were on average more related to one another than individuals outside the core area, within Lot 2 (permutation test, $P = 0.001$, Table 3). It is noteworthy that the relatedness between all females and males within the core area, and between all females and males outside, is 0.126 (± 0.014, ± 0.168); whilst the relatedness between the core area and all females and males outside is zero, significantly lower than within all females and males in the core area. This indicates some dispersal of related animals. With the exception of Lot 8, animals resident in areas outside KOCP were on average not related with each other.

Parentage

Parentage was analysed for 16 individuals (Table 4). DNA was available for between 12 and 14 candidate mothers (mean 12.8), and for between 9 and 16 candidate fathers (mean 11.2). From field observations, we estimate that

Table 3 Mean pairwise relatedness r_{xy} (Queller & Goodnight 1989; ± SD for r_{xy} and ± SD_j, jackknifed over 13 loci), within and between demographic units of orang-utans (all adult females (f_{all}), flanged ($m_{flanged}$) and unflanged adult males ($m_{unflanged}$), all adult males (m_{all})). Mean relatedness values within units (n_{ind}: number of individuals; n_{pair}: number of pairs) were statistically compared by permutation tests using 1000 permutations for each test

Unit 1			Unit 2			Between units	
	n_{ind}, n_{pair}	mean $r_{xy, \text{unit 1}}$ (± SD_j, ± SD)		n_{ind}, n_{pair}	mean $r_{xy, \text{unit 2}}$ (± SD_j, ± SD)	P (mean $r_{xy, \text{unit 1}}$ – mean $r_{xy, \text{unit 2}}$)	mean $r_{xy, \text{unit 1 vs. 2}}$ (± SD_j, ± SD)
$f_{all, s.s.}$	12, 66	0.148 (± 0.018, ± 0.183)	$m_{all, s.s.}$	11, 55	0.142 (± 0.018, ± 0.179)	0.45	0.085 (± 0.015, ± 0.158)
			$m_{flanged, s.s.}$	6, 15	0.103 (± 0.058, ± 0.198)	0.34	0.069 (± 0.018, ± 0.166)
			$m_{unflanged, s.s.}$	5, 10	0.136 (± 0.067, ± 0.174)	0.49	0.104 (± 0.015, ± 0.147)
$m_{flanged, s.s.}$	6, 15	0.103 (± 0.058, ± 0.198)	$m_{unflanged, s.s.}$	5, 10	0.136 (± 0.067, ± 0.174)	0.38	0.164 (± 0.015, ± 0.0.172)
$f_{all, s.a.}$	3, 3	0.303 (± 0.222, ± 0.222)	$m_{all, c.a.}$	5, 10	0.305 (± 0.029, ± 0.128)	0.36	0.236 (± 0.030, ± 0.164)
$f_{all, outside}$	9, 36	0.076 (± 0.019, ± 0.139)	$m_{all, outside}$	6, 15	0.065 (± 0.027, ± 0.162)	0.45	0.045 (± 0.013, ± 0.158)
f&$m_{all, c.a.}$	8, 28	0.268 (± 0.028, ± 0.155)	f&$m_{all, outside}$	15, 105	0.059 (± 0.009, ± 0.151)	0.001	0.126 (± 0.014, ± 0.168)
f_{all}	14, 78	0.114 (± 0.007, ± 0.171)	f&m_{lot02}	26, 325	0.060 (± 0.005, ± 0.174)	0.058	0.055 (± 0.008, ± 0.168)
			f&m_{lot04}	20, 190	−0.002 (± 0.008, ± 0.188)	0.004	−0.030 (± 0.006, ± 0.172)
			f&m_{lot05}	20, 190	0.003 (± 0.006, ± 0.185)	0.002	0.002 (± 0.005, ± 0.0.166)
			f&m_{lot07}	7, 21	0.052 (± 0.021, ± 0.173)	0.16	0.003 (± 0.011, ± 0.165)
			f&m_{lot08}	5, 10	0.151 (± 0.075, ± 0.258)	0.32	0.073 (± 0.015, ± 0.0.181)
			f&m_{lot10}	17, 136	0.005 (± 0.009, ± 0.198)	0.011	−0.021 (± 0.009, ± 0.0.169)

s.s.: study site (core study area + extension study area); c.a.: core study area; outside: extension study area; all: all individuals from one area; Lot 2 to Lot 10: Lots 2, 4, 5, 7, 8 and 10 of the LKWS from the same riverside as the KOCP study site.

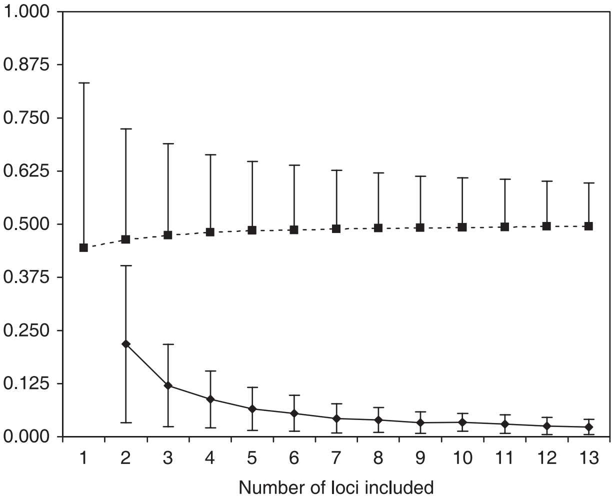

Fig. 2 Relationship between the number of loci used and mean relatedness $r \pm SD$ (dashed line) and the difference between consecutive relatedness $r \pm SD$ estimates (solid line), analysed using rarefaction analysis with 10 000 simulations of parent–offspring relationships with expected $r = 0.5$.

80% of candidate mothers and 67% of candidate fathers were sampled. The combined exclusionary power of the 13 loci used was 0.993 for the one-parent scenario and 0.9998 for the second-parent scenario.

The combined exclusion/kinship analysis assigned 12 mothers and eight fathers. Seven females and six males were assigned on the basis that they were the only sampled candidate parents with allelic matches at all loci. Two candidate females and two males were assigned on the basis of a significant parent–offspring kinship, and four candidate females and one male were assigned based on the presence of only one female/male pair without any exclusions. Parameters for the maximum-likelihood analysis (CERVUS) were estimated directly from the data. Due to the high consistency of genotypes identified in independent repeats, we estimated the genotyping error as 1% or less. The proportion of successful genotypes at 13 microsatellites was 99.7% using success rates from the 139 samples, which were genotyped for each locus seven times. The probability that the true parents were sampled is likely to be inversely related with the age of the offspring for which parentage was analysed. The number of candidate mothers and fathers with no exclusions was inversely correlated with the age of the offspring tested (Table 3; Pearson's correlation coefficient $r_{corr} = –0.58$ and $r_{corr} = –0.52$, respectively). We considered this sampling bias by a conservative estimation of the total number of candidate parents and the proportion of nonsampled candidate parents. We adopted the maximum number of observed candidate mothers and fathers for any offspring as the number of candidate parents for all tested offspring (14 and 16 candidate mothers and fathers, respectively). From field observations, we estimated that an additional 25% and 50% of candidate parents remained un-sampled for offspring conceived between 1990 and 2000, and for offspring conceived earlier. We allowed

Table 4 Parentage in KOCP study site analysed by combined exclusion/kinship analysis and maximum likelihood analysis of the likelihood ratio (LOD) of the most likely vs. the second most likely parent. Three hierarchical criteria were used to assign candidate parents for the combined exclusion/kinship analysis. Assignment of parents was first by combined exclusion/kinship analysis (EK) and by maximum-likelihood analysis (CERVUS) and then by assignment using both approaches jointly. Parentage was finally accepted when both analyses, EK and CERVUS, concurred or by CERVUS only in cases where EK could not distinguish between several possible candidate parents. For details and explained examples, see text

	No candidates			Combined exclusion/kinship analysis†					Assigned mothers			Accepted fathers		
Offspring (estimated year of birth)	♀	♂	Observed mother	# ♀ without excl.	# ♀ with sig. kinship‡	# ♂ no excl.	# ♂ with sig. kinship‡	# pairs without excl.	EK (♀)	CERVUS (♀, LOD score, significance§)	Final assign^{mt} (Y/N)	EK ♂††	CERVUS (♂††, LOD, approach‡‡, significance§)	Final assign^{mt} (Y/N)
I17 (1990)	13	9		1 m	0	2	2	0	I26	I5, 4.2, +^{ex1}	N	—	I15$_{f}$, 4.31, uc, +^{ex1}	N
I2 (1998)	14	16	I1	1 m	0	3	1 d	1	I1	I1, 3.1, *	Y	SsL2.4$_{uf}$	SsL2.4$_{uf}$, 10.88, c, *	Y
I22 (1999)	14	16	SsL2.36	3	2	1 d	0	1 m	SsL2.5	SsL2.5, 4.6, +	SsL2.36¶	I16	I16, 4.9, c, *	N¶
I24 (1990)	12	9		2	0	1 d	0	1 m	SsL2.5		N	SsL2.3$_{f}$	SsL2.3$_{f}$, 3.5, uc, *	Y
I25 (1990)	12	9		1 m	0	2	0	1 d	I8	I8, 2.6, +	Y	I4$_{f}$	I4$_{f}$, 7.1, c, *	Y
Ss11 (1985)	12	9		0	0	0	0	0	—	—	N	—	—	N
Ss13 (1990)	12	9		2	1 m	1 d	0	1	Ss8	Ss8, 4.8, +	Y	Ss12$_{f}$	Ss12$_{f}$, 5.6, c, +	Y
Ss2 (1985)	13	9		1 m	1	0	0	0	SsL2.9		N	—	—	N
Ss3 (1985)	12	9		2	1 m	1 d	1	1	I26	I26, 6.55, *	Y	I19$_{f}$	I19$_{f}$, 6.6, c, +	Y
Ss7 (1990)	13	9		0	0	2	0	0	—	I8, 0.5, +^{ex2}	N	—	I4$_{f}$, 4.1, uc, +	Y
Ss9 (2000)	14	16	Ss8	2	0	1 d	0	1 m	Ss8	Ss8, 4.1, +	Y	I19$_{f}$	I19$_{f}$, 8.5, c, +	Y
SsL2.10 (1985)	12	9		1 m	1	0	0	0	SsL2.36	—	N	—	I15$_{f}$, 1.1, uc, +^{ex1}	N
SsL2.2 (1999)	14	16		2	0	1 d	1	1 m	SsL2.20	I1, 2.9, +	N	Ss12$_{f}$	Ss12$_{f}$, 5.6, uc, +	Y
SsL2.33 (1998)	14	16	SsL2.5	4	2	2	0	2	—	SsL2.5, 5.3, +	Y	—	I19$_{f}$, 5.9, c, +	Y
SsL2.37 (1990)	12	9		1 m	1	2	1 d	1	I5	I5, 4.7, +	Y	I16$_{f}$	I16$_{f}$, 6.6, c, *	Y
SsL2.4 (1985)	12	9		1 m	1	0	0	0	I23	I23, 4.6, +	Y	—	I15$_{f}$, 0.7, c, +^{ex1}	N
Number of accepted mums / dads									12	12	9	8	13	10

†The criterion used for accepting mothers and fathers according the combined exclusion/kinship analysis is indicated as m for mothers and d for fathers.

‡Number of females or males that are significantly ($P < 0.05$) more likely to conform to the null hypothesis of parent–offspring relationship vs. the alternative hypotheses of a half-sibling relationship.

§Relaxed (+, 80%) and strict (*, 95%) criteria for significance were applied. Shown are only individuals with significant LOD scores.

¶Despite that both genetic approaches identified SsL2.36 as mother, SsL2.36 was accepted based on behavioural observations (see text). Although male I16 was accepted by both analyses, there were five pair exclusions when SsL2.36 was considered the true mother. Consequently, we excluded from the final assignment of paternity.

††Fathers were either flanged$_{f}$ or unflanged$_{uf}$ at the time of conception.

‡‡CERVUS analysis was conducted either unconditional or conditional on the genetically identified mother.

^{ex1} and ^{ex2}: accepted by maximum-likelihood (CERVUS) analysis despite one and two exclusions, respectively.

candidate parents to be related to one other at the level suggested by the relatedness analysis amongst males and amongst females in the main study area ($r_{xy} = 0.14$). Cervus identified 12 females to be the most likely mothers and 13 males to be the most likely fathers, significant at the 80% level.

Eight assigned maternities were consistent using both the combined exclusion/kinship and the maximum-likelihood analysis. These cases included three out of four females that were identified as potential mothers from behavioural observations. The genetically identified mother of I22 (SsL2.5) did not concur with the mother identified by behavioural observations (SsL2.36). The inference of SsL2.5 as genetic mother was relatively weak by combined exclusion and kinship analysis, as it was based solely on the observation that SsL2.5 was the only female with no pair exclusions taken together with male I16, who was the only candidate father without exclusions. Cervus identified SsL2.36 as the mother at the 80% level, and supported parentage of male I16 at the 95% level. Behavioural observations clearly identified SsL2.36 as mother whilst excluding SsL2.5, because SsL2.5 mothered another offspring in the previous year (also confirmed by the genetic data). Consequently, we conclude that the genetic parentage assignment was incorrect in this instance. In two cases, SsL2.2 and I17, cervus included a different mother from the combined exclusion/kinship at the 80% level. Cervus also included a mother, I5, at the 80% level for Ss7, despite two exclusions. We accepted maternity only for the 12 mothers where both analyses concurred.

All seven sires identified by the combined exclusion/kinship analysis were also identified by cervus as the most likely fathers at the 80% level. Cervus analysis additionally included five fathers where the combined exclusion/kinship approach was unable to exclude all but one male. In three cases, the same male, I15, was identified, despite exclusions. To be conservative, we did not assign this male as a sire. The 10 father–offspring pairs identified involved six different sires, five of which were flanged and one, SsL2.4, was unflanged. SsL2.4's parentage was supported by the highest LOD score observed in cervus for the whole data set, and by a significant kinship analysis.

Relatedness between assigned mothers and offspring ($r_{xy} = 0.42 \pm 0.12$, $n = 9$), and between assigned father and offspring ($r_{xy} = 0.37 \pm 0.11$, $n = 10$), were much smaller than theoretically expected ($r = 0.5$).

Discussion

These data are the first to examine fine-scale genetic structure in Bornean orang-utans. Intensive sampling and genotyping using 13 microsatellite loci produced high parentage exclusion probabilities. Paternity and maternity assignment was concordant between two methodological approaches, exclusions analysis and maximum-likelihood analysis, which are based on different assumptions. The low estimated relatedness values between offspring and assigned mothers and fathers were smaller than theoretically expected, but this bias is commonly observed (e.g. Altmann *et al*. 1996; Bradley *et al*. 2005), and is likely to be caused by the inclusion of unknown relatives in the population that was used to calculate the baseline allele frequencies for relatedness estimation (Queller & Goodnight 1989).

Relatedness and dispersal

Behavioural studies by Rodman (1973), MacKinnon (1974), Rijksen (1978), Galdikas (1985a), Mitani (1989), van Schaik & van Hooff (1996), and Singleton & van Schaik (2002) suggest female philopatry and male dispersal. The orang-utan's arboreal habits, long life-span and correspondingly slow life history result in the slow accumulation of demographic data. In addition, its dispersed social system means that interactions between individuals are rarely observed, and many aspects of orang-utan social structure remain unknown (Singleton & van Schaik 2002). Behavioural observations of orang-utan dispersal from the natal range are extremely rare. However, females appear to settle in ranges overlapping those of their mothers (Rodman 1973; Mitani 1989; Galdikas 1995), and physically similar females form clusters with a high degree of range-overlap (Singleton & van Schaik 2002). Conversely, males appear to disperse at maturity, and most new individuals observed entering or passing through long-term study areas are males (MacKinnon 1974; Galdikas 1985a; van Schaik & van Hooff 1996). Males appear to range more widely than females, and their ranging reflects the local abundance of sexually attractive females (Singleton & van Schaik 2002). Thus the available behavioural and demographic data suggest that dispersal may be male biased in semi-solitary orang-utans, and that female-biased dispersal in social African great apes (including humans) evolved after the separation from orang-utans. Orang-utans could thus represent the 'ancestral state' of sociality from which the complex social systems of the other great apes derive (Kappeler *et al*. 2002; Baker *et al*. 2004).

However, our genetic data show that orang-utans exhibit similar levels of relatedness in both sexes for resident animals and for the entire population. The mean pairwise relatedness values for adult males and adult females show similar values among the two sexes for: (i) the entire population ($r_{xy} = 0.142$ for males vs. $r_{xy} = 0.148$ for females); (ii) the resident population ($r_{xy} = 0.305$ for males vs. $r_{xy} = 0.303$ for females); and (iii) the nonresident population ($r_{xy} = 0.065$ for males vs. $r_{xy} = 0.076$ for females). This finding supports the hypothesis that both sexes disperse (or remain natal) in a similar way. Comparable findings have been described for a Sumatran orang-utan population living in the Ketambe study site, Gunung Leuser National Park (Utami *et al*. 2002). Both sample sites are of similar size (450 ha for Ketambe vs. 400 ha for Kinabatangan), and a similar number of adult individuals were sampled for the genetic analysis: 17 adults (11 males, 6 females) in Ketambe and 23 (11 males, 12 females) in Kinabatangan. Both studies failed to support the hypothesis that males disperse more than females.

In Ketambe, the relatedness values for males and females were negative, suggesting that both sexes were mainly unrelated. In Kinabatangan, relatedness values were positive for the entire study population (see above, with mean r_{xy} value for the entire population = 0.114). Values documented within the core area are extremely high, but were much lower for nonresident animals (see above). Our results suggest that both sexes have similar migration patterns and are philopatric, and that highly related individuals tend to remain in the same area for both sexes. The number of animals identified in the 4 km^2 area of the KOCP core study area supports the 'social arena' hypothesis (Rijksen & Meijaard 1999); i.e. animals living in the same area maintain loose relationships together, which justifies the term of 'semi-solitary' species (see also Sugardjito *et al*. 1987; Mitani *et al*. 1991). For the first time, our genetic data demonstrate that animals tend to live in communities of related individuals for both sexes (mean r_{xy} for males and females in the core study area = 0.268). However, the observed pattern might be the result of the drastic habitat fragmentation process that has taken place in the Kinabatangan floodplain over the past few decades (Goossens *et al*. 2005, 2006), preventing males from dispersing. As the mean r_{xy} values are lower than expected ($r_{xy} = 0.42 \pm 0.12$ and 0.37 ± 0.11, respectively, for mothers and fathers; also reported elsewhere, e.g. Bradley *et al*. 2005), there is no indication of inbreeding. Clearly, the variance is too high to comment on those single dyads where observed r was above 0.5.

We observed substantial heterozygote excess and negative F_{IS} values for all loci, indicating a small number of breeders in the population (Pudovkin *et al*. 1996). Orang-utan life history is the slowest among extant great apes (Wich *et al*. 2004), with females reaching sexual maturity between 11 and 15 years of age in the wild, and first breeding not occurring until several years later (Delgado & van Schaik 2000). We identified potential mothers for each adolescent individual in the population, as predicted if solitary adolescents are relatively newly independent from their mothers, and have not yet dispersed from their natal area. We were also able to identify the mothers for three of four unflanged males sampled within the study site. This may be a consequence of males delaying dispersal until they are large unflanged adults, or may be due to the fragmented state of the Kinabatangan forest and its recent reduction in size (Ancrenaz *et al*. 2004b; Goossens *et al*. 2005). This latter possibility might also explain an observed high density of adult males in the area (three resident flanged males and two resident unflanged males in the 4-km^2 study site; three nonresident flanged males and three nonresident unflanged males observed during the sampling period). Interestingly, no potential sires could be identified for unflanged males, suggesting that the period between birth and sampling is critical in finding fathers in the surrounding population, possibly as a result of adult male death.

Male reproductive success

Our data confirm the finding of Utami *et al*. (2002) that both unflanged and flanged males can sire offspring. This is in accordance with behavioural data showing that both male morphs consort with females, although unflanged males do so less often than flanged males (e.g. Sumatran orang-utans, Utami 2000; Bornean orang-utans, Galdikas 1985a, b). Both flanged and unflanged Bornean males force copulation with females, while flanged Sumatran males have rarely been observed to do so (reviewed in Delgado & van Schaik 2000). There may also be more flanged males in Bornean populations than in Sumatran orang-utans (Delgado & van Schaik 2000), which may be expected to influence patterns of distribution of male reproductive success.

Female orang-utans also employ complex social and mating strategies, impacting upon male reproductive strategies. For example, Bornean females spend less time associated with one another than Sumatran females, which may influence male mating strategies (Galdikas 1985a; van Schaik 1999; Wich *et al*. 1999). Females also show a marked preference for mating with flanged males (Schürmann 1982; Utami 2000), exhibit tactics to reduce sexual harassment (Fox 2002), and participate in long-term bipartite relationships (Delgado & van Schaik 2000). Finally, female tactics may also differ with the stability of the social environment; for example, it is interesting to note that the unflanged males in the study by Utami *et al*. (2002) sired offspring during 'unstable periods' when an irregular flanged male entered the area and challenged the regular flanged male, and hence all males mated opportunistically (Utami 2000).

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