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Male orang-utan bimaturism and reproductive success at Camp Leakey in Tanjung Puting National Park, Indonesia

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Abstract Unlike most mammals, male orang-utans exhibit bimaturism, in that mature individuals express one of two distinct morphological forms. Socially subordinate, 'unflanged' males are comparable to females in their size and facial morphology, while socially dominant 'flanged' males exhibit extreme sexual dimorphism and secondary sexual characteristics, primarily in the form of cheek pads ('flanges'). Although male ornaments in other species are often phenotypically plastic, such characteristics in orang-utans are irreversible—and, given that both morphs are sexually mature and can father offspring—their adaptive significance remains unclear. We determined paternity of orang-utans at Camp Leakey in Tanjung Puting National Park, within the home range of one long-term dominant male, Kusasi, before, during and after his period of dominance, in comparison with subordinate male conspecifics. We found that Kusasi fathered substantially more offspring conceived during his dominant period than any other male and that socially subordinate, unflanged males only fathered offspring during periods of rank instability. We conclude that orang-utan male bimaturism is consistent with an evolutionarily stable reproductive strategy and that reproduction within the range of a dominant, flanged male is highly skewed in his favour, while unflanged males may largely wait for reproductive opportunities.

Keywords Male bimaturism · Sexual selection · Secondary sexual characteristics · Paternity · Reproductive success

Introduction

Orang-utans (*Pongo* spp.) exist in a semi-solitary society with roving promiscuity (van Schaik and van Hooff 1996), in which the relatively smaller, philopatric home ranges of females are enveloped by those of dispersing adult males (Galdikas 1985a; van Noordwijk et al. 2012). Such males exhibit bimaturism, expressing one of two morphological forms (Fig. 1). Socially subordinate, 'unflanged' male orang-utans have typically reached sexual maturity by 14 years of age, yet appear similar to adult females in their size and facial morphology (MacKinnon 1974, 1979; Galdikas 1985b). In contrast, socially dominant 'flanged' males develop large and irreversible secondary sexual characteristics, primarily in the form of bidiscoid cheek pads (flanges) and a laryngeal sac (throat pouch) (Rodman and Mitani 1987; Utami Atmoko and van Hooff 2004). Flanged males also grow near-ceaselessly in size throughout their entire lives: They commonly weigh in excess of 80 kg, more than twice the weight of females (Markham and Groves 1990; Leigh and Shea 1995). Although male home ranges may overlap, only a single flanged male is typically dominant in any given area, in which he is intolerant of other flanged males (Galdikas 1981,

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Fig. 1 An unflanged, socially subordinate male orang-utan (*center*) appears similar in facial morphology to a female orang-utan (*left*). In contrast, a socially dominant flanged male (*right*) demonstrates secondary sexual characteristics, primarily in the form of enlarged bidiscoid cheek pads. Both male morphs are sexually mature and both can father offspring. Photos: M Block (*left*), Bpk Bain (*center*, *right*)

1985a, c). Flanged males usually tolerate their unflanged conspecifics but are thought to suppress their maturation. The underlying psychoneuroendocrinological mechanism for male bimaturism is yet to be fully understood (Kingsley 1982; Maggioncalda et al. 1999, 2000, 2002; Emery Thompson et al. 2012).

Male bimaturism in orang-utans is unusual—if not unique—among mammals, in that maturation from unflanged to flanged male morph is an irreversible change. Such developments in male morphology are more often phenotypically plastic and alter with dominance rank, such as colorations in vervet monkeys (*Chlorocebus pygerythrus*, Gerald 2001) and mandrills (*Mandrillus sphinx*, Setchell and Dixson 2001), 'fattedness' in mandrills (Wickings et al. 1993) and ventral staining in Verraux's sifaka (*Propithecus verreauxi verreauxi*) (Lewis and van Schaik 2007). The irreversibility of maturation from an unflanged to a flanged male orang-utan is notable given the apparent disadvantages experienced by flanged individuals. Such males have greater nutritional and energetic demands, inhibited locomotion, higher levels of stress and increased inter-male aggression, all of which may be the product of their extreme sexual dimorphism (Mitani et al. 1996). Further, transitioning males must still assert their dominance over concurrently developing rivals: Failure to become dominant may require a newly flanged male to leave the area, risking further aggressive encounters with other flanged males in the search for a new home range (Galdikas 1985c; Utami Atmoko et al. 2009b). Nonetheless, given that such elaborate ornaments as cheek pads typically indicate an element of female choice, it is commonly hypothesized that male orang-utan bimaturism arose as the product of sexual selection: That cheek-padded males prove more attractive to females and thus benefit from greater reproductive success (Schürmann and van Hooff 1986; Rodman and Mitani 1987; Utami et al. 2002; Utami Atmoko and van Hooff 2004; Goossens et al. 2006; Mitra Setia and van Schaik 2007; Knott et al. 2010).

This theory is complicated, however, by the fact that both flanged and unflanged males are known to copulate with females and father offspring (Utami et al. 2002; Goossens et al. 2006). Flanged males tend to 'sit and wait' for females to approach their vicinity and mate with them co-operatively (Schürmann and van Hooff 1986; Utami et al. 2002). While flanged males have also been observed to force copulations with unwilling females, such behaviour is more typical of unflanged males (Galdikas 1981, 1985b; Schürmann and van Hooff 1986; Fox 2002), though there is considerable variation across study sites (Knott 2009; Utami Atmoko et al. 2009a). Consequently, rather than being an alternative reproductive strategy of unflanged males, it is probable that forced copulation is a contingent response to resistance by females, who may vary in their willingness to copulate irrespective of male morphology (Knott et al. 2010). At Ketambe in Sumatra, Utami et al. (2002) found that unflanged males fathered more than half (six) of 11 sampled offspring born over 15 years and were particularly reproductively successful when male dominance relationships appeared to be unstable. Two flanged males were consecutively dominant within this time, respectively fathering one of four, and both of two, offspring born during their periods of dominance (Utami et al. 2002). In Kinabatangan in Sabah, Malaysian Borneo, Goossens et al. (2006) assigned paternity for eight offspring. One was fathered by an unflanged male, while five different flanged males achieved the remaining paternities. In Goossens et al.'s (2006) study, the dominance status and morphology of fathers had not been observed over time. Nonetheless, it is clear from both studies that dominant flanged males failed to individually father a significantly greater proportion of offspring born during their period of dominance than multiple subordinate flanged or unflanged males. The adaptive significance of male bimaturism therefore remains unclear (Utami Atmoko et al. 2009a).

The sample sizes in these studies were small: It is uncertain if these results would represent behaviour in larger or better-sampled populations. Further, Utami et al.'s (2002) study comprised multiple reintroduced, nulliparous females whose behaviour may not fully represent that of wild conspecifics—and, while Goossens et al.'s (2006) study focused entirely on a wild population—the large number of dominant males sampled presents only a snapshot of reproductive success over relatively short periods of dominance (Utami Atmoko et al. 2009a). Given that speciation is thought to have occurred at least 400,000 years ago (Locke et al. 2011)—and that Bornean and Sumatran orang-utans have since diverged into geographically and reproductively isolated island populations—it is also possible that the findings from either study may not be applicable to the other species (Goossens et al. 2006). In particular, there are thought to be more flanged males in Bornean than Sumatran populations and reduced incidence of developmental arrest among Bornean male orang-utans (Delgado and van Schaik 2000; Dunkel et al. 2013). As sexual dimorphism is often correlated with polygyny in multiple taxa (Alexander et al. 1979; Clutton-Brock 1985; Weckerly 1998), it is possible that orang-utans were once gregarious with 'harems' of females controlled exclusively by a single male (van Hooff 1995). Notably, Harrison and Chivers (2007) proposed that historic climate change might have resulted in extreme fruit paucity, triggering a more solitary lifestyle and opening a niche for an opportunistic 'sexual predator' in the form of unflanged males. However, for the evolution of male bimaturism to be adaptive, an advantage is required for flanged males over unflanged conspecifics to offset the associated costs. It is puzzling why two morphological forms persist, unless both have significant advantages.

In this study, we genetically quantify the role of bimaturism in male orang-utan reproductive success at Camp Leakey in Tanjung Puting National Park, Central Kalimantan, Republic of Indonesia. Specifically, we test the hypothesis that Kusasi, the dominant flanged male from 1995 to July 2006, fathered substantially more offspring conceived in his home range during his period of dominance than any other male.

Materials and methods

Study site and population

Camp Leakey was established by Galdikas and Brindamour in 1971 as an orang-utan research and reintroduction site (latitude 111° 57′ to 112° 1′ E; longitude 2° 45′ to 2° 48′ S), within a surrounding study area of 50 km^2 (Fig. 2). At least 90 ex-captive and displaced orang-utans of near-equal sex ratio were released there from 1971 until 1985 (Yeager 1997; Galdikas and Ashbury 2013), complementing a wild population of around 6000 individuals (Singleton et al. 2004). The number of orang-utans living in the study area, and thus comprising the study population, cannot be practically quantified over the long term: Inevitably, the population demographics have fluctuated over the site's 43-year history. However, ex-captive females were typically observed to stay in or adjacent to their area of reintroduction, thus mimicking the philopatry observed in their wild-born female conspecifics (Galdikas 1985a). All wild and ex-captive males, both flanged and unflanged, were found to range far beyond the study area when observed over multiple years. Though Kusasi ranged extensively while unflanged, his home range as a dominant male is known to have been approximately 10 km^2 in size, larger than the minimum home ranges estimated for consubspecifics at other sites (Sabangau 5.6 km^2, Gunung Palung 6.5 km^2; Utami Atmoko et al. 2009b). Kusasi's home range radiated outward from Camp Leakey and was therefore wholly encompassed by the study area.

Camp Leakey's contemporary study population includes approximately 60 orang-utans that range within the vicinity of the site and within Kusasi's home range, comprising ex-captives, wild orang-utans and their wild-born offspring. All have been behaviourally monitored for up to 43 years, typically since their reintroduction or birth, and many frequently return to the site, accompanied by third- and fourth-generation individuals. As a result of long-term behavioural monitoring by Galdikas, most orang-utans at the camp can be identified, and it is known when many reached maturity, when males developed their cheek pads, and when females gave birth to their offspring. On the basis of direct observations of dyadic interactions, Camp Leakey's dominant males are known to have included Ralph (1983–1991), Bagong (1991), Adik (1991–1992), Yayat (1992–1995), Kusasi (1995–2006), Win (2006) and Tom (2006–present). Of these, Ralph and Win were entirely wild orang-utans, and Tom is the wild-born son of an ex-captive, reintroduced female. The remainder comprise wild-born ex-captives.

Sample collection

Faecal samples were collected from all orang-utans observed in the 50 km^2 study area, during formal research visits to the site from June to November 2008 and from October 2010 to February 2011. Each orang-utan was identified twice, independently, by at least two experienced observers who agreed on the individual's identity. Orang-utans were followed until they defaecated. Samples were collected immediately and only when defaecation was directly witnessed and were preserved in ethanol followed by desiccation with silica (Nsubuga et al. 2004). In order to confirm identifications, faecal samples were preferentially collected from multiple defaecations of the same purported individual, identified on separate occasions.

Genotyping and parentage analyses

Genomic DNA was extracted for at least one faecal sample from each independent defaecation, using the QIAamp DNA Stool Mini Kit (Qiagen)—or, when insufficient DNA could be extracted—using a modified 2CTAB/PCI protocol that has been shown in prior studies to be effective in such cases

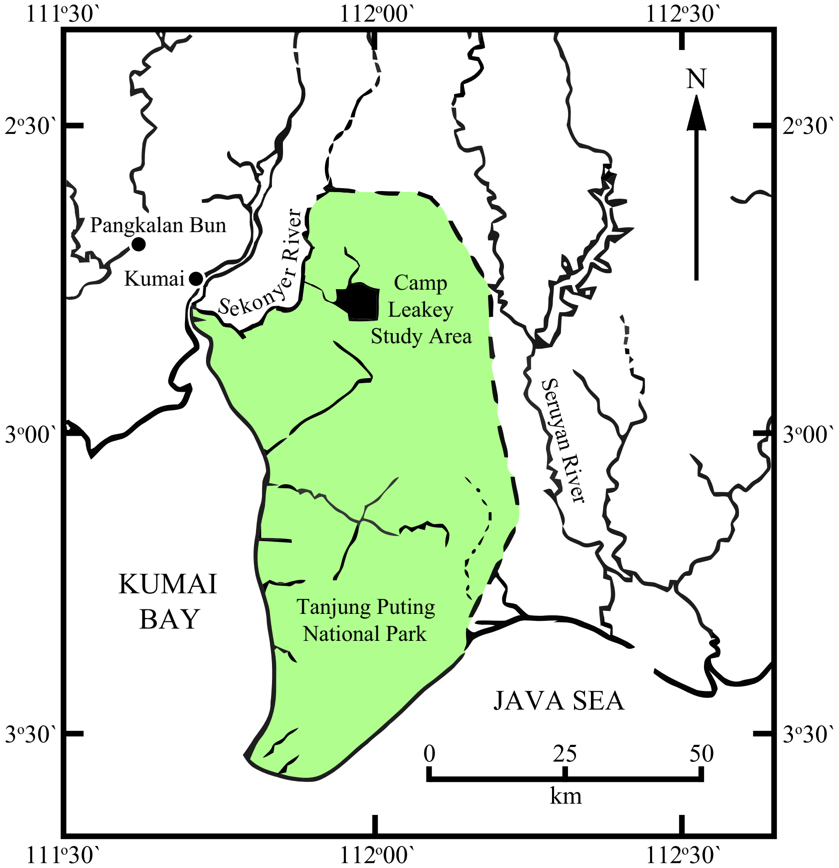

Fig. 2 Approximate location of Camp Leakey and the surrounding study area, on the southernmost promontory of Central Kalimantan, Indonesian Borneo. Adapted from Galdikas (1978)

(Vallet et al. 2008). A panel of 14 autosomal tetranucleotide microsatellite loci were selected; of these, 3 were species-specific (Nietlisbach et al. 2010) and 11 had amplified successfully in a range of primates, including orang-utans, in previous studies (Zhang et al. 2001; Kanthaswamy and Smith 2002; Utami et al. 2002). These loci, plus two sex-linked loci (Di Fiore 2005), were co-amplified in an initial multiplex PCR, with dilutions of the resulting products re-amplified in singleplex PCRs with fluorescently labeled forward primers and unlabeled reverse primers. Microsatellite amplification procedures followed those described in Arandjelovic et al. (2009). Locus information, primer sequences, annealing temperatures, labels and references are all included in Table S1 of the data supplement. Alleles were sized using an ABI PRISM 3130xl Genetic Analyzer relative to a 400HD ROX-labeled internal size standard and scored manually with GeneMapper 3.7 (Applied Biosystems). For each extract, DNA was quantified following the procedures of Morin et al. (2001). The required number of PCR replicates was then performed to maintain error rates of less than 1 % when scoring homozygotes, as determined by Arandjelovic et al. (2009). Heterozygotes were scored by observing both alleles in at least two independent PCRs.

The program MICRO-CHECKER 2.2.3 was used to examine genotypes for allelic dropout, null alleles and scoring errors due to stuttering (van Oosterhout et al. 2004). An exact test for Hardy-Weinberg equilibrium was performed in GENEPOP 4.3 (Rousset 2008), with Bonferroni correction to a significance level of $p<0.05$. The same program was used to test for linkage disequilibrium, using only the genotypes of orang-utans known to be unrelated and unidentified individuals not philopatric to the study area. Given that this region includes known population substructure, multiple parent-offspring pairs and both full- and half-sibling dyads—all of which are known to increase false linkage declarations (Slate and Pemberton 2007)—it is unlikely true synteny of loci could be assessed using all genotypes.

In CERVUS 3.0 (Kalinowski et al. 2007), probability of identity among siblings (PID-sibs) values were computed for each locus, to determine the minimum number of loci necessary to obtain a combined value of <0.001—thus ensuring with confidence that matching samples purported to derive from the same individual did indeed derive from a single source (Waits et al. 2001). Genotypes purported to derive from the same individual, which mismatched at three or fewer loci, were re-examined for possible genotyping errors and re-genotyped where necessary to resolve potential ambiguities. Matching samples were given a consensus ID and genotype for use in subsequent analyses. Average non-exclusion probabilities were computed for identity of two unrelated individuals, for identity of two siblings, for one candidate parent when neither parent is known and for one candidate parent given the genotype of a known parent of the opposite sex.

Maternity analyses were first conducted with an exclusionary approach in CERVUS 3.0, in which offspring from known mother-offspring pairs were required to share one allele at each locus with the putative mother. In subsequent paternity analyses, offspring were required to share one allele at each locus with a candidate father, and—where mother-offspring pairs were known and confirmed—the second allele with the mother.

To accommodate genotyping errors, null alleles and potential mutations, parentage was also inferred using a likelihood approach. Parentage was simulated over 100,000 offspring in the same program, to obtain critical values of delta at confidence levels of 80 % (relaxed) and 95 % (strict) (Kalinowski et al. 2007). We tested a wide range of values for the proportion of fathers sampled, eventually choosing 0.5 in the final simulation, given that results were robust to the different values tested. Candidate fathers comprised all those that were alive and at least 5.5 years old at the time of the offspring's conception, this age being the youngest at which captive males are thought to have achieved paternities (Porton 1997). Candidate offspring included all those who could potentially have been fathered by at least one of the candidate males, with conception calculated as having occurred between 227 and 301 days prior to parturition—the widest, and thus most conservative, published range of gestation periods (Brandt and Mitchell 1971). Paternity was then inferred from this simulation, for which non-exclusion probabilities and delta scores were computed for each trio. To further consider parentage assignments, analyses were repeated in the program COLONY 2.0.5.7, which jointly infers parentage and sibships across the entire pedigree configuration, rather than for pairs of individuals (Jones and Wang 2010). For input parameters, we chose a fully polygamous mating system with no inbreeding, 'long' length of run with 'high' precision, no allele frequency updating and no sibship prior.

Length of dominant period

On 6 June 2003 and 8 June 2004, Kusasi was anaesthetized at Camp Leakey for emergency veterinary surgery to attend to infected wounds—presumably following fights with unknown males—and was subsequently followed during periods of prolonged recovery. To acknowledge that these veterinary interventions may have artificially extended Kusasi's tenure as the dominant male, we also tested our hypothesis with a shortened period of dominance, from 1995 to June 2003. As we discuss, without such interventions, it is unlikely that Kusasi would have naturally survived to maintain his dominant status.

Results

A total of 45 unique genotypes were generated from the extracts at 12 microsatellite loci. These loci, plus their summary statistics, are listed in Table S2 of the data supplement. Of these, the locus D1S550 was observed to sporadically amplify non-target DNA when scoring alleles; it was therefore removed from analyses. The mean proportion of individuals typed was 0.9556 across the remaining 11 loci, representing 39 known and identifiable orang-utans and six of unknown identity. Data at a total of 10 microsatellite loci were necessary to sufficiently distinguish individuals with a PID-sibs value of <0.001. The average non-exclusion probabilities for identity of two unrelated individuals, and for identity of two siblings, were 4.50E-0010 and 1.52E-04, respectively. The combined probability of excluding a random individual from parentage was 0.022 when neither of the two parents is known and 0.001 when one parent is known. Consequently, the 11 loci were considered sufficiently numerous and polymorphic to infer parentage reliably. No evidence was found of null alleles, allelic dropout, scoring error due to stuttering or deviation from Hardy-Weinberg equilibrium in the final dataset. Linkage disequilibrium was not detected in a subset of 20 genotypes, comprising 14 unrelated orang-utans and 6 unidentifiable individuals not thought to be philopatric to the study area.

With the exception of one flanged male (UK6), all orang-utans were sampled within Kusasi's home range. The sex, reproductive status and relatedness of the 45 individuals sampled, plus details of their use in analyses, are shown in Tables S3–S4 of the data supplement. In brief, in 1995—at the start of Kusasi's dominant period—the individuals sampled comprised at least three infant, two juvenile and one adolescent offspring; two nulliparous, two primiparous and eight multiparous females; and one flanged and two unflanged males. By 2003, they included 6 infant and 5 juvenile offspring; 4 primiparous and 11 multiparous females; and 3 unflanged and 3 flanged males. By 2006, they included 6 infant and 5 juvenile offspring, 4 nulliparous and 15 multiparous females, and 3 unflanged and 4 flanged males. A further six identifiable males were sampled from 2008, including two flanged, two unflanged, one juvenile/unflanged male and one undergoing the transition from unflanged to flanged male morph. The sampled individuals include multiple generations of offspring.

Parentage was inferred using a minimum of six loci, to accommodate the least-typed individual. In practice, parentage was determined from 8 to 11 loci, as detailed in Table 1. Only eight loci were used for just two individuals, for whom the mothers were known and genotyped. For these eight loci, the combined probability of excluding a random individual from parentage was 0.0063 when one parent is known.

Table 1 Parentage assignments for orang-utans at Camp Leakey, ordered by birth year of offspring and thus grouped by dominant flanged male

Number of loci at which candidates excluded											Cervus			Colony
Offspring	Loci	Birth year	N_C	Kusasi	Ponorogo	Sampson	UK1	Pan	Father	Dominant	P_e	Delta		Prob.
Tom	10	1983	1	3	–	–	–	–	–	Ralph	–	–	–	–
Riga	11	1983	1	2	–	–	–	–	–	Ralph	–	–	–	–
Uranus	11	1984	1	0	–	–	–	–	–	Ralph	–	–	–	–
Gina	11	1987	2	2	–	–	–	–	–	Ralph	–	–	–	–
Peta	11	1990	5	1	–	–	–	–	–	Ralph	–	–	–	–
Sampson	11	1993	6	0	–	–	–	–	Kusasi^{f}	Yayat	0.9926	4.32E+00	*	0.9983
Pan	10	1995	8	0	5	–	3	–	Kusasi^{f}	Yayat/Kusasi	0.9883	4.86E+00	*	1.0000
Chandra	11	1996	8	8	2	2	–	–	–	Kusasi	–	–	–	–
Randy	11	1996	8	8	2	4	4	–	–	Kusasi	–	–	–	–
Uning	11	1996	8	0	4	–	3	–	Kusasi^{f}	Kusasi	0.9944	3.74E+00	*	0.9920
Nova	8	1997	9	0	1	1	0	0	Kusasi^{f}	Kusasi	0.9641	2.29E+00	+	0.9673
Aria	11	1999	9	0	5	4	3	–	Kusasi^{f}	Kusasi	0.9978	5.99E+00	*	1.0000
Ashley	10	2000	10	0	5	1	4	–	Kusasi^{f}	Kusasi	0.9660	2.09E+00	+	0.9785
Raymond	11	2000	10	0	2	2	1	–	Kusasi^{f}	Kusasi	0.9984	6.36E+00	*	1.0000
Rimba	11	2000	10	0	4	2	2	–	Kusasi^{f}	Kusasi	0.9975	6.20E+00	*	1.0000
Thomas	11	2000	10	0	4	1	3	–	Kusasi^{f}	Kusasi	0.9901	3.94E+00	*	0.9923
Percy	8	2001	11	0	5	1	3	0	Kusasi^{f}	Kusasi	0.9789	4.92E-01	+	0.9997
Gajah Mada	11	2003	12	5	5	5	5	4	–	Kusasi	–	–	–	–
Goldie	10	2004	12	1	0	3	2	2	Ponorogo^{uf}	Kusasi♦	0.9995	4.17E+00	*	0.0562
Toronto	11	2005	12	3	4	1	4	4	–	Kusasi♦	–	–	–	–
Reiner	11	2005	12	2	4	1	1	2	Sampson^{uf}	Kusasi♦	0.9981	1.53E+00	+	–
Nirvana	11	2005	12	4	4	3	1	3	–	Kusasi♦	–	–	–	–
Tiido	10	2006	12	1	7	4	3	0	–	Kusasi♦/Win	–	–	–	–
Putri	11	2007	16	2	0	3	3	3	Ponorogo^{uf}	Tom	0.9997	8.69E+00	*	0.2182
Thor	11	2009	17	3	4	2	0	3	UK1^{uk}	Tom	0.9999	9.63E+00	*	0.4883

‘*Loci*’ indicates the number of loci typed per offspring; ‘N_C’ the number of candidate fathers tested for each offspring. Only candidate fathers who were assigned paternities with either the exclusion or likelihood approach are included in columns in the matrix. Eight candidate offspring whose identities or birth years could not be confirmed, and for whom paternities could not be inferred, are excluded from the table. P_e is exclusion probability as calculated in CERVUS 3.0 using allele frequencies from all individuals; an *asterisk* (*) indicates that a given trio delta value meets the strict 95 % confidence level, + indicates the relaxed 80 % confidence level. ‘Prob.’ is the probability that the parentage assignment is correct, as inferred by COLONY 2.0.5.7. ‘Dominant’ denotes the dominant male at the time of the offspring’s conception; two names indicate a transitory period in dominance. ^{f} denotes flanged at the time of the offspring’s conception; ^{uf} denotes unflanged at the time of the offspring’s conception; ^{uk} denotes male morph unknown at the time of the offspring’s conception, but flanged in 2011. A *diamond* (♦) denotes rank instability as a result of Kusasi’s ongoing and invasive veterinary treatment, from 2003 to 2006. ‘−’denotes that no data are available, i.e. parentage was not inferred, or males were not considered as candidate fathers due to them not being of reproductive age at the time of the offspring’s conception

Maternity analyses confirmed 25 mother-offspring pairs known from life history data. No previously unrecognized mother-offspring pairs were observed. Up to 17 candidate fathers were included in paternity analyses; of these, only 12 were known and identifiable males. At the time of sample collection, 10 of the candidate fathers were unflanged, two were in the process of developing their cheek pads, and five had full secondary sexual characteristics. Aside from Kusasi and his successor, Tom—whose cheek pads developed in 2005—these flanged males were rarely recorded in the study area, and so it is not known when they developed their cheek pads.

Paternity could be assigned to 14 of 33 candidate offspring, conceived across multiple decades. Of these, four were inferred by CERVUS at the relaxed, 80 % confidence level; the remainder were accepted with at least 95 % statistical certainty. The most likely fathers inferred by COLONY were in accordance with those inferred by CERVUS, with one exception: COLONY could not identify a father for one offspring (Reiner), for which CERVUS had inferred paternity at the relaxed confidence level. The 14 offspring were fathered by Kusasi (N=10), Ponorogo (N=2), Sampson (N=1) and ‘UK1’ (N=1), a male undergoing the transition from unflanged to flanged male in 2011, who could not be specifically identified at the time of sample collection (Table 1). Ponorogo is a wild orang-utan who was unflanged but of indeterminate age at the time of each offspring's conception. Sampson is the wild-born, second-generation offspring of an ex-captive, reintroduced female, who was 12 years of age at the time of Reiner's conception. On three occasions, Pan—the wild-born, first-generation offspring of an ex-captive, reintroduced female—could not be excluded as a father. However, given that Pan was inferred to be Kusasi's son, it is probable that the similarity of their genotypes precluded Pan's exclusion. In two of these cases, the likelihood approach of both CERVUS and COLONY inferred Kusasi to be the father of the offspring. Of the five candidate fathers that were flanged at the time of sample collection, only Kusasi achieved paternities. Non-dominant males were especially reproductively successful during periods of rank instability and towards the beginning and end of periods of established dominance rank (Table 1).

When considering Kusasi's nominal period of dominance (1995–July 2006), paternity could be assigned for 65 % of offspring (*N*=17). Nine were fathered by Kusasi (53 %), one by Ponorogo (6 %), one by Sampson (6 %) and six by unsampled males (35 %). Based on manual examination of genotypes, the six offspring for which paternity could not be inferred were fathered by numerous males and not by a single rival to Kusasi.

Without the major veterinary intervention in June 2003, Kusasi would likely have been unable to maintain reproductive or social dominance. It is therefore more appropriate to consider the abbreviated period from 1995 to June 2003. Of the 12 offspring conceived during this time period, Kusasi fathered nine, while the remaining three were fathered by unknown males. Thus, Kusasi fathered 75 % of all offspring conceived during his period of unequivocal dominance (1995–June 2003). Kusasi fathered only one of the six offspring sampled that were conceived prior to him becoming dominant in 1995. He fathered none of the seven genotyped offspring conceived after June 2003, subsequent to the veterinary intervention.

Discussion

Irrespective of the length of time that he was considered truly 'dominant', Kusasi fathered substantially more offspring than any other male during his tenure as dominant male and substantially more than he did before or after his dominant period. Although Kusasi fathered one of the six sampled offspring conceived prior to him becoming the dominant male, he had recently become flanged at the time of that offspring's conception. The lack of paternities achieved by Kusasi following 2003 can likely be attributed to his reduced efficacy as dominant male, as the result of frequent human monitoring and veterinary interventions that reduced his independence and autonomy. During this period, Kusasi spent considerably more time in the immediate vicinity of Camp Leakey's buildings, was sometimes fed alone and individually and received both antibiotics and topical medication for infected wounds on his head and face: Such incidents became increasingly prevalent over time.

In contrast with earlier findings (Utami et al. 2002), therefore, our results indicate that this dominant flanged male enjoyed greater reproductive success than his unflanged or subordinate flanged conspecifics during his period of dominance, within his home range. Our observation that multiple males achieve paternities during periods of rank instability—that is, towards the beginning and end of Kusasi's dominant period—supports prior findings (Utami et al. 2002) and is probably the consequence of opportunistic mating in the absence of a dominant male. It is possible that unflanged males achieved paternities in distant, unsampled areas of Kusasi's range, that are not represented in our study. Given that we sampled comprehensively throughout his home range, and far beyond this in the wider study area, however, it is thought that most orang-utans that might live in Kusasi's home range are represented in this study. The number of individuals sampled (45) differs from the contemporary population (60), as 4 years have elapsed since samples were last collected: Many new infants have been born in this time that are not relevant to our hypothesis. The difference also incorporates females whose genotypes are equally unimportant, on the basis that they were born—and gave birth to their offspring—many years or decades prior to Kusasi becoming reproductively active. Consequently, our results are not consistent with the expectations of prior hypotheses, such as that of 'alternative tactics', in which the strategies of flanged (sit-and-wait) and unflanged (go-and-search) male orang-utans are equally successful reproductively (Utami et al. 2002). In contrast, our evidence implies an evolutionarily stable strategy, in which unflanged males simply bide their time until periods of rank instability.

Our results also support theories of female choice. Strategies that allow a female to choose their mate may be especially important in orang-utans, given that their interbirth intervals are the longest of any mammalian species. Females typically give birth once every 8 years (Galdikas and Wood 1990) and rarely produce more than four offspring in their lifetime (Galdikas 1981). Monopolization of females—and thus greater reproductive success—is commonly thought to be a principal benefit of dominant status in males (van Noordwijk and van Schaik 2004). However, in orang-utans, it is impractical for dominant males to achieve this independently (Utami Atmoko et al. 2009a). The semi-solitary nature of orang-utans, combined with vast male home ranges, severely inhibits a male's ability to monitor females outside of lengthy consortships (Galdikas 1985c). Simply finding females to monopolize, in the absence of female vocalizations, may potentially be challenging. While intrasexual selection is theoretically important—in the form of increased body size, which equips a male to intimidate or outcompete his rivals—it is not directly correlated to their reproductive success, as male orang-utans with the largest bodies are not certain to become dominant over their smaller rivals. Consequently, we believe that it is more logical to assume that Kusasi's heightened reproductive success was ultimately achieved through inter-sexual selection, in the form of female preference for flanged males.

At Camp Leakey, female orang-utans are observed to copulate frequently with unflanged males: However, overall, we report few conceptions. Such findings support those from other sites: Notably, that females in Gunung Palung National Park were found to mate co-operatively with unflanged males only when not ovulating and thus least likely to conceive (Knott et al. 2010). As a lack of perineal swelling during oestrus (Galdikas 1981) is presumed to create paternity confusion, willingness of non-conceptive females to copulate might facilitate relationships with unflanged males, in preparation for when they mature (Schürmann and van Hooff 1986). Nonetheless, limited evidence may also indicate that unflanged males more commonly achieve paternities with nulliparous females (Borneo G L Banes, unpublished data; Sumatra Utami Atmoko et al. 2009a), whose first infants are subject to higher mortality rates (Kuze et al. 2012). This might explain observations of greater proceptive behaviour exhibited by nulliparous females to unflanged males, in contrast with older, parous females (Schürmann 1982; Galdikas 1981, 1985b; Rodman and Mitani 1987). It is not clear if this reflects female choice—that parous females elect to conceive with flanged males—or if flanged males prefer to invest in procreating with parous, experienced females with proven reproductive abilities. Preference by dominant males for parous and multiparous females has been observed in a wide range of primate taxa (Anderson 1986). Notably, in multimale gorilla groups, dominant males have been documented to mate more frequently with cycling adult females, while subordinate males achieve mating success primarily with female subadults (Robbins 1999). It is further possible that apparent assortative mating of flanged males with adult females and unflanged males with adolescent, nulliparous females could be an emergent property of male dominance, with flanged males sequestering the most valuable females (Utami Atmoko et al. 2009a).

It is possible that, among the many features distinguishing flanged and unflanged males, cheek pads specifically may not only be important in female choice but might also serve alternative or additional functions. Numerous studies have hypothesized that these ornaments could play a role in auditory communication (Short 1981; Galdikas 1983), but these theories are yet to be empirically tested. Cheek pads might also facilitate olfactory communication, though extensive studies of this hypothesis are yet to prove conclusive (T. E. Goodwin, unpublished data). Indeed, it is difficult to comprehensively address female choice in primates, given that so few exhibit ornaments for which females might express preference. In orang-utans, small sample sizes combine with the lack of robustness that often characterize studies of female choice.

It is possible that the reproductive behaviour of the orang-utans at Camp Leakey may not be characteristic of their wild conspecifics. Though the camp's orang-utans comprise largely wild-born individuals, descended from ex-captives reintroduced in the 1970s, their circumstances are atypical. Orang-utans at Camp Leakey continue to be provisioned up to twice a day, and many interact with the human visitors and staff that frequent the site. Furthermore, as evidenced by Kusasi, numerous orang-utans have received medical treatment for injuries that may have otherwise proved fatal. It is therefore plausible that such human intervention has shaped the social structure among orang-utans at Camp Leakey. In particular, this may have influenced the identity and longevity of the dominant male, although Kusasi was found to be substantially more reproductively successful even in advance of his medical interventions. In spite of this, the majority of orang-utans live fully independent lives, and all are free to range into the forest whenever they choose to do so. Notably, Kusasi elected to live independently of humans within 24 h of his arrival at Camp Leakey as a juvenile, chose not to participate in active rehabilitation and had no direct involvement with human caregivers—aside from provisioning later in life—until the medical interventions documented in this study, long after becoming dominant male. Indeed, the majority of orang-utans do not interact with humans, do not attend daily feedings and may disappear for extended periods without returning to the site. Consequently, Camp Leakey's orang-utans exhibit behaviour close to that of wild populations, to the fullest possible extent.

Though our paternity data are few, this research represents the largest longitudinal orang-utan paternity study to be conducted to date, in situ, in a single population. Given the slow demographic histories of orang-utans, further monitoring and genetic studies will be needed at Camp Leakey over the very long term in order to provide new information on male reproductive competition and female choice. This hypothesis might then be revisited, to determine if Tom—the incumbent dominant male—enjoys comparably significant reproductive success.

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