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Orangutan mating behavior and strategies

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16.1 Introduction

In species where both sexes are more or less solitary, such as orangutans, mating requires that at

least one sex find the other. The mating system of orangutans is of interest because it is based on an interaction between female choice and male harassment and coercion, against a background of

intense male-male competition, which has produced extreme sexual dimorphism and is accompanied by very unusual male bimaturism.

The aim of this chapter is to assess how these three aspects of sexual selection (male competition, female choice and mating conflict) interact to produce the mating behavior of orangutans. After a theoretical introduction and a review of what is known about orangutan mating behavior, we present a compilation of basic data from various sites in order to assess whether the broad picture built up over the years is similar throughout the orangutan's geographic range.

Orangutans have a semi-solitary life style. Individuals usually live alone in highly overlapping home ranges, and at some sites they occasionally aggregate in large fruit trees or groves (see Chapter 17). During times of high fruit abundance, these aggregations develop into travel bands, in which individuals travel together in a coordinated fashion (Sugardjito *et al.* 1987; Utami *et al.* 1997; van Schaik 1999; Singleton and van Schaik 2002). Consortships, a form of travel band in which a male-female pair may range together in a coordinated way for several days, weeks or even months and engage in sexual behavior, are seen at all sites. Other individuals (females, unflanged males and adolescent individuals) may also associate around a consort pair (Schürmann and van Hooff 1986), although fully mature, flanged males never associate together and usually behave antagonistically toward each other (see Chapter 15).

Orangutans have three striking features for primates: (1) extreme sexual dimorphism in body size, (2) forced matings, and (3) bimaturism among males. As in many other dimorphic primate species, the sexual dimorphism in body size arises because males continue to grow beyond the age at which females stop growing. In orangutans, male growth continues gradually until well after the twentieth year of age ('indeterminate growth', Leigh and Shea [1995]). In addition to larger body size, the male secondary sexual characters (SSCs) consist of flanged cheeks and a throat sack, with which they can produce long calls to advertise their presence (MacKinnon 1974; Rijksen 1978; Rodman 1984; Galdikas 1985b).

Hypotheses to explain sexual dimorphism invoke sexual selection in which female choice or

male-male competition predominate (Schürmann and van Hooff, 1986; Rodman and Mitani, 1987). Between-male contest competition must clearly have contributed to the development of the extreme sexual dimorphism of this species. Indeed, Rodman and Mitani (1987) proposed it as the sole factor. However, because females selectively approach or allow themselves to be approached by flanged males when they are in their fertile periods, 'female choice' must also play a critical role in maintaining male physical characteristics.

Another unusual feature of the mating system of orangutans is the occurrence of forced matings ('rapes') (Rijksen 1978; Galdikas 1979, 1985b, c; Mitani 1985a, b; Fox 1998, 2002). Even though pre-mating aggression and physical coercion to mate are seen in other primates, orangutan females seem to resist mating attempts by particular males much more strongly than seen in other species. Mating resistance, in which a female struggles and attempts to prevent intromission while the male attempts to restrain the female by grabbing and holding on to her arms, legs and body, can result in a fierce physical fight between a male and a female (and sometimes her youngest offspring). These interactions may involve hitting, pushing and biting by all involved and whimpering, squealing, grumphing, kiss-squeaking and other vocalizations by the female and/or her offspring. The level and timing of female cooperation and resistance is variable: some male mating attempts may start with resistance and continue passively or even cooperatively, others may start cooperatively but end with resistance (Fox 1998), making classification complicated. Since females resist mating attempts by particular males even when no other males are present (and may not even be within hearing distance) this behavior is unlikely to incite direct male-male competition as suggested for other species with conspicuous female mating resistance (*e.g.* Cox and LeBoeuf 1977; Boness *et al.* 1982) but seems to be an honest reflection of female preference (Fox 1998, 2002). So far, in all populations females have been observed to engage in a wide range of mating interactions from female-initiated active participation to fiercely contested, with many variations in between.

Perhaps the most unusual feature of orangutans is the remarkable individual variation in the age

at which sexually mature males develop their SSCs—a phenomenon called bimaturism (Uchida 1996; Maggioncalda *et al.* 1999, 2002). In some males, at least in Sumatra, this development may be delayed until the male is well over 30 years old (Utami Atmoko 2000; Utami *et al.* 2002), some 20 years after reaching sexual maturity and at least 15 years after reaching the size of adult females. Although these unflanged or 'arrested' males lack SSCs, they are fertile, sexually active and able to sire offspring (Kingsley 1982; Maggioncalda *et al.* 1999, 2002; Utami Atmoko 2000; Utami, *et al.* 2002). This bimaturism leads to the coexistence of two adult, sexually mature morphs: flanged and unflanged males.

The presence of an uncontested flanged male has been proposed as a key proximate factor maintaining developmental arrest in unflanged males, at least in captivity (Kingsley 1982; Graham and Nadler 1990; Maggioncalda *et al.* 1999, 2002; Utami Atmoko 2000). However, this is unlikely to work in the wild, where the two kinds of males inhabit large ranges widely overlapping with those of many others, flanged and unflanged. Utami *et al.* (2002) could show that two early hypotheses for the evolution of bimaturism were inconsistent with the data. The data reviewed in this chapter can be used to evaluate other hypotheses (see discussion).

This chapter considers the mating strategies of males and females and their interactions, based on field studies in Ketambe (Sumatra), Suaq Balimbing (Sumatra), Gunung Palung (West Kalimantan), Tanjung Puting (Central Kalimantan), Sabangau (Central Kalimantan), Tuanan (Central Kalimantan), Kutai (East Kalimantan) and Kinabatangan (Sabah). Table 16.1 gives an overview of the database used for this chapter.

16.2 Mating behavior of orangutans

16.2.1 Ontogeny of mating behavior

Mating behavior is not unique to adult and adolescent individuals. In Ketambe, infants as young as two years of age, of either sex, already show keen interest in sexual behavior. For instance, the infant male Yossa sometimes masturbated as part of his play behavior, sometimes using his own hands or feet, once using a stick, and occasionally even thrusting into his mother's vagina while she was hanging. Immatures also directed sexual behavior at each other, especially when they were playing. For instance, 6-year-old female Tati had 3-year-old Yossa masturbate her, and after that she masturbated him. During rest, orangutan mothers often licked their infant's genitals to clean them, and this may be the first sexual experience for

Table 16.1 Overview of the database used for this chapter

Site	Period	Researchers
Sumatra		
Ketambe	1972–1978	H.D. Rijksen, C.L. Schürmann
	1979–1996	Ketambe orangutan project Universitas Nasional Jakarta—Utrecht University Netherlands
Suaq Balimbing	1994–1999	Suaq Balimbing orangutan project Universitas Indonesia Jakarta—Duke University USA
Borneo		
Kinabatangan	2000–2003	M. Ancrenaz, S.S. James
Kutai NP	1981–1982	J. Mitani (1985b)
Sabangau	2003–2005	H. Morrogh-Bernard
Tuanan	2003–2006	Tuanan orangutan project Universitas Nasional Jakarta—University of Zürich, Switzerland
Tanjung Puting	1971–1975	B.M.F. Galdikas (1979, 1981, 1985a, b)
Gunung Palung	1994–2003	C.D. Knott

*See the Preface and Chapter 7 for descriptions of habitat.

young individuals. They also acquire early knowledge of mating behavior by watching their mothers copulate with males. Especially unflanged males occasionally try to mate with mothers with small infants; infants almost always respond to these attempts by struggling with the male.

16.2.2 Male mating behavior

Male-male competition has been cited as a major determinant of orangutan social organization, in which males compete for access to females (Rodman 1973b, 1988; Rijken 1978; Galdikas 1979; Mitani 1985a; Utami Atmoko 2000; Utami Atmoko *et al.* in preparation; see Chapter 15). In support of this argument, flanged males are highly intolerant of each other, and their 'long calls' function as a spacing mechanism (Mitani 1985a; Mitra Setia and van Schaik 2007; see Chapter 15). These same long calls also function as a locator call to females, and attract receptive females (Mitra Setia and van Schaik 2007; see Chapter 17). Receptive females may initiate association by approaching a male's long call, or accept his initiative to associate (Schürmann and van Hooff 1986; see Chapter 17). Unflanged males, on the other hand, cannot attract females through vocalizations and have to actively

search for females. Thus the mating strategies of the two different male morphs differ considerably in the way they find potential mates.

To see whether males have more copulations with females who are potentially receptive than with females in a non-reproductive stage (clearly pregnant or nursing a dependent infant), we counted the number of their copulations with females in either stage. Figure 16.1 shows that, at all sites, flanged males copulate more with potentially fertile females than with non-fertile females. Unflanged males show a weaker tendency, but more detailed data are needed to detect whether there are real differences between male morphs and populations.

A consortship occurs when a male and a female travel together and show coordination in their behavior for several days or weeks, up to a month, during which interactions, including copulations, may take place (MacKinnon 1974; Rijksen 1978; Utami Atmoko 2000). Data from several sites suggest that adult (parous) females prefer flanged males as consort partners (Galdikas 1979, 1981; Mitani 1985b; Rodman and Mitani 1987; Mitra Setia 1995; Fox 2002). This is confirmed by the available quantitative data for Ketambe, Sumatra (Fig. 16.2): almost one half of the copulations by unflanged

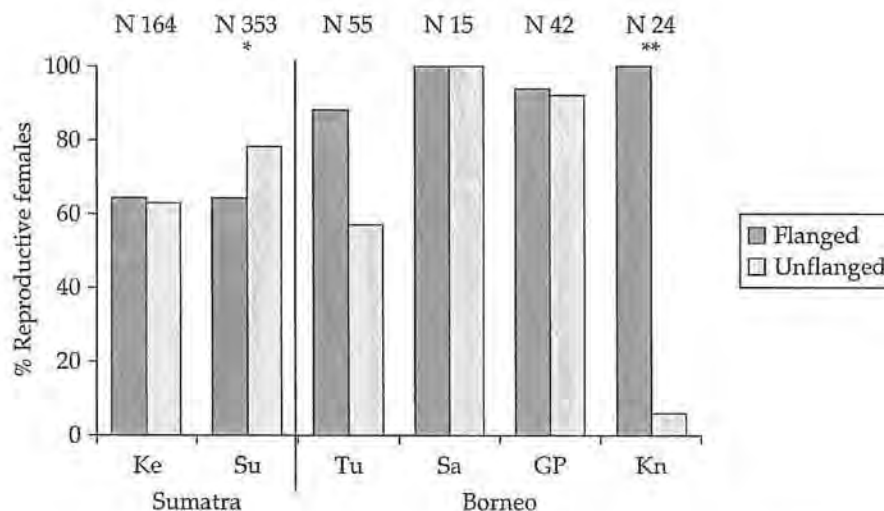


Figure 16.1 Percentage of copulations by flanged and unflanged males with reproductive (sexually active) females in six different sites. Numbers above columns indicate total number of copulations observed and stars indicate significant difference between flanged and unflanged males in G_{adj} -test: * $p < 0.05$; ** $p < 0.01$.

males are not linked to consortships (of at least 5 hours duration), roughly three times as much as for flanged males. The very limited sample from Sabangau suggests the same pattern there as well. The reason is that unflanged males are frequently unable to successfully mate-guard a female for a long time, since the consortships are often involuntary, maintained only by the male, and an encounter with a more dominant male (either unflanged or flanged) terminates the consortship. However, even unflanged males in Ketambe and Sabangau achieve the majority of copulations in consortships rather than during brief encounters. This suggests that both male morphs attempt to mate-guard when they get the chance, but flanged males may be more successful because they have no or fewer competitors and they may be preferred company by females who endure less sexual harassment in their proximity (Fox 2002).

Even when males mate-guard a particular female this relationship does not completely exclude others: in Ketambe, Sabangau and Gunung Palung flanged males occasionally engage in extra-consort copulations (ECC), that is, during a consortship they copulate not only with their consort partner, but also with another female (temporarily) present in the same party. In Ketambe, most ECCs happened while the consort pair visited a large fruit tree (most often fig trees) in which other orangutans were already aggregated (Utami *et al.* 1997;

Utami Atmoko 2000). Unflanged males were never observed to have an ECC in either site.

In Ketambe, females were found more often in the proximity of the dominant male than of other flanged males; their associations with him lasted longer as well (Utami and Mitra Setia 1995; Mitra Setia 1995). Likewise, in Suaq, non-dominant flanged males were very rarely found in consortship and had negligible mating success (van Schaik 2004). However, Ketambe females maintained a good relationship not only with a dominant flanged male but also with some unflanged males (Utami Atmoko 2000). Tolerance of unflanged males by flanged males was sometimes observed, even during consortships of a flanged male and a receptive female (cf. Rijksen 1978; Galdikas 1985b, c; Mitani 1985b; van Schaik and van Hooft 1996). In Ketambe, for example, it has been observed that the flanged male Jon allowed the unflanged male Boris to travel within 20 m distance for several days while he was in consort with the adult female Yet (Utami Atmoko 2000; Utami Atmoko *et al.* in preparation). In such situations females have been seen to have ECCs with an unflanged male (Utami Atmoko 2000; Utami Atmoko *et al.* in preparation).

16.2.3 Female mating behavior

Female orangutans mate promiscuously, not only with flanged males other than the dominant male but especially with unflanged males (Rijksen 1978; Galdikas 1985b, c; Rodman and Mitani 1987). Early reports suggested that females mated cooperatively with the flanged male that is resident within her home range (Schürmann 1982; Galdikas 1985b; Schürmann and van Hooft 1986), whereas unflanged males usually obtained matings by force (Galdikas 1985b; Rijksen 1978; Rodman and Mitani 1987). However, occasionally, females demonstrated the reverse pattern, displaying proceptivity toward some unflanged males (Fox 1998; Utami Atmoko 2000) and resisting mating attempts by flanged males (Rijksen 1978; Mitani 1985b; Knott and Kahlenberg 2007).

Quantitative data from multiple sites (Fig. 16.3) show more variation in mating patterns than previously thought: females in the Sumatran and at least

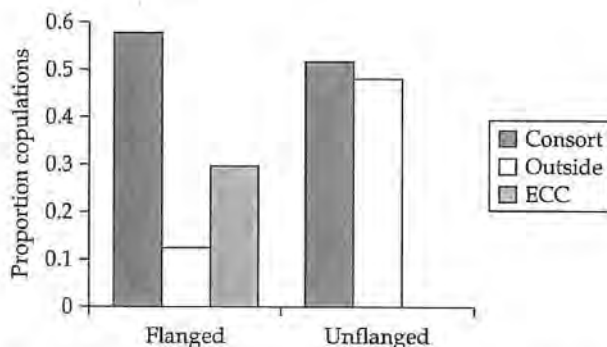


Figure 16.2 Distribution of copulations by flanged and unflanged males over three different contexts (ECC, extra-consort copulation) in Ketambe. Even though the two male morphs have a significantly different distribution over three categories ($G_{adj} = 22.0$ $P < 0.001$), the proportion of copulations during consort vs other context did not differ significantly ($G_{adj} = 2.07$ NS).

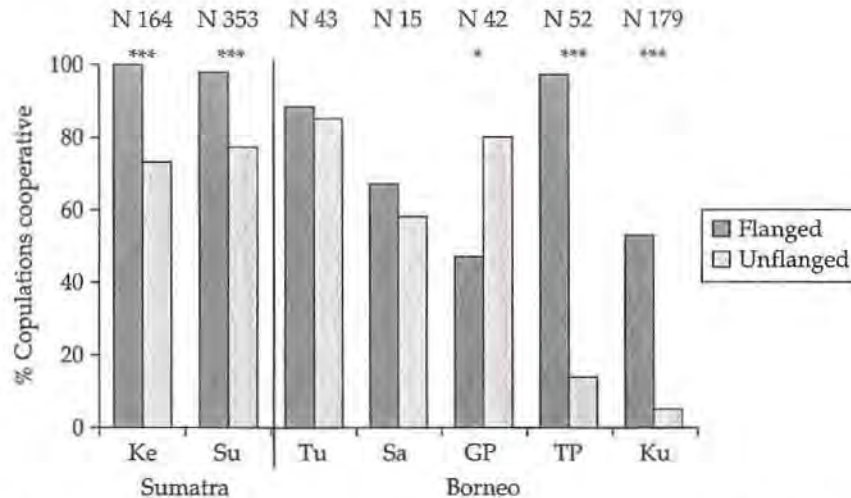


Figure 16.3 Percentage of copulations by both flanged and unflanged males that are cooperative (i.e. non-resisted by females) in seven sites. Numbers above columns indicate total number of copulations observed and stars indicate significant difference between flanged and unflanged males in G_{adj} -test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

two of the Bornean sites cooperate in the majority of all copulation attempts. In both Sumatran and most Bornean sites, except for Gunung Palung, cooperative matings by females are significantly more likely with flanged males than with unflanged males (see Fig. 16.3). However, in most Bornean sites, females do resist a higher proportion of mating attempts by flanged males than in Sumatra, supporting the idea that females in both Sumatra and Borneo have a preference for mating with flanged males. However, the differences in female cooperation rates for mating with the two male morphs are variable and for the Bornean sites based on small numbers of females. Whether a female resists a particular mating attempt probably depends not only on the status and morph of the male, but also on other factors, such as female parity and the relationship between the partners.

Females in association with a non-preferred male can play an active role in ending the association, even when they cannot 'outrun' an agile unflanged male, who tends to intercept her when she flees (e.g. van Schaik 2004). Females can travel in the direction of recent long call by dominant males and thus orchestrate a male-male encounter (Utami and Mitra Setia 1995; Fox 2002). Fox (1998, 2002) found in Suaq a clear decrease in mating attempts by unflanged males when females stayed

in the proximity of a flanged male. Thus, despite a vulnerability to harassment caused by their semi-solitary lifestyle, orangutan females not only resist particular mating attempts, they also can manipulate mating success of non-preferred males by manoeuvring themselves under the protective umbrella of a dominant male. This reasoning also implies that the unflanged males are in a 'waiting-room' situation, making the best of the bad job. In other words, the unflanged stage is not a permanent alternative tactic but a transitional stage (Utami Atmoko and van Hooff 2004).

16.3 Paternity

So far, only two studies described the genetic consequences of the mating strategies of flanged and unflanged males, one in Sumatra (Utami *et al.* 2002), and one in Borneo (Goossens *et al.* 2006b). These studies used human-derived microsatellites to estimate paternity, and showed that both unflanged and flanged males are successful in siring offspring. In Ketambe, paternity analysis of 11 offspring born over a 15-year period was carried out and 6 out of 10 offspring could be attributed to 3 unflanged males and 4 to 3 flanged males in the area at the time of conception of these offspring (the father for the eleventh offspring could not be

Table 16.2 Overview of the database used for this chapter identified sires for 10 infants born during study period in Ketambe. Infants (columns) in italics are from rehabilitant matriline, others from wild local matriline. Males (rows) present in year of conception in study area; names in capitals refer to flanged males, in lower case to unflanged males. P, present, P*, identified as sire.

	<i>Ans</i>	<i>Pet</i>	<i>Chris</i>	<i>Her</i>	<i>Eib</i>	<i>Puji</i>	<i>Yos</i>	<i>Set</i>	<i>Gen</i>	<i>Kel</i>	Dominant male
Year born	1975	1983	1987	1988	1991	1991	1992	1993	1997	1996	
JON	P	P*	P	P	P	P					1972–1990
NUR		P				P	P*	P*			1991–1995
ERIK		P	A	P	P	P	P				
MIKI				P	P	P	P	P			
W		P			P						
I		P		P	P						Old male?
JAN									P		1995 attempt?
BORIS									P	P	1995–?
DOBA											
BOBBY									P*		
AZ											
Boris	P*	P	P	P*	P*	P	P	P			
Bas				P	P	P	P	P			
Wiba					P						
X						P*	P	P	P	P*	
Dedi									P	P	
Aldo			P*		P						

identified) (see Table 16.2). At least, the available data show that most or all infants were sired during voluntary consortships, even if these were not with flanged males.

The results from Ketambe suggest roughly equal per capita siring success of unflanged and flanged males (Utami *et al.* 2002), but this conclusion needs some qualification. First, six offspring were sired by three (of at least six known) unflanged males. One of these unflanged males sired three infants and eventually developed SSCs and became the dominant flanged male in the area. Second, five of the ten offspring with an identified father were from matriline whose founding females were ex-rehabilitants released at Ketambe in the 1970s (see Rijksen 1978). Only one of these five was sired by a flanged male and none by the then-dominant flanged male in the area. Third, at least four of the six offspring sired by unflanged males were born to nulliparous mothers, and only one flanged male is known to have sired a first-born offspring of a wild mother in this sample.

These two latter points may well be related. At Ketambe, Schürmann (1982) studied the socio-sexual development of an adolescent female. He noted a slow and very gradual process of developing relations between the maturing young female and males. Young unflanged males were the first to show interest in her and they formed voluntary consortships with her. The adolescent female, however, showed a clear preference for the bigger, flanged males, in particular for the biggest one in the area, who in turn only gradually developed an interest in her. It took a long time, at least 5 years, for the adolescent female to build up a relationship, which involved consortship and mating with the dominant local flanged male using various kinds of soliciting behavior. It was not until the last year before she conceived that this dominant local flanged male started to react to her elaborate proceptive behavior with 'male presenting'. Flanged males appeared much more interested in older parous females, who showed less pronounced proceptive behavior (Schürmann, 1982). Observations

at Suaq (van Schaik, unpublished data) paint very much the same picture, and concur with findings for chimpanzees (Muller *et al.* 2006), and primates in general, that males prefer parous over nulliparous females (Anderson 1986). Rehabilitant females, being better fed than their wild counterparts, may have matured faster (cf. Knott 2001), and thus have become pregnant while still in the phase of voluntary consortships with unflanged males. In conclusion, then, the high siring success of unflanged males may be due to a high proportion of first-borns, especially to females of the ex-rehabilitant matriline.

Furthermore it should be noted that three of four infants sired by a flanged male were offspring of the local dominant and wild local females, the fourth was the offspring of an ex-rehabilitant mother. Since one to four other flanged males were present in the area during the conception periods, this suggests a clear advantage to the dominant flanged male over non-dominant flanged males in achieving paternity.

Goossens *et al.* (2006b) performed a similar paternity analysis in the 4-km² study site in the lower Kinabatangan floodplain. Parentage was analyzed for 16 individuals, but paternity could be assigned for only six offspring (compared to 10 in Utami *et al.* 2002). One out of six offspring could be attributed to an unflanged male, the five others could be attributed to flanged males, but no additional information on the mothers was available.

16.4 Discussion

16.4.1 Male-male competition and female choice

Flanged males advertise their location by giving long calls and can thus attract females to come to them, whereas unflanged males have to actively travel through an area to locate potentially fertile females. Overall, and certainly in Sumatra, the majority of sexual interactions were cooperative and occurred during a consort relationship. However, females everywhere resist a proportion of mating attempts. Since these resisted matings generally occur in the absence of other males they are assumed to reflect honest female preference for

or aversion to particular males (Fox 2002). Thus, females select their sexual partners and choose when to cooperatively consort and mate. A close social relationship built up during consorts seems to be of importance for cooperative and probably also for successful copulation. Since female orangutans show no visible estrus signs, it must be the changes in their behavior and additionally olfactory signals that induce the male to mate or at least to cooperate (Schürmann 1982).

Genetic paternity studies in the field (Utami *et al.* 2002; Goossens *et al.* 2006b) confirm observations from zoos that unflanged males are able to sire offspring. However, even though more data are needed, it appears unflanged males were most successful in siring offspring with nulliparous females. Other studies relying on behavior to estimate paternity suggested that the resident dominant flanged male fathered all or most offspring of females within his home range (Rodman 1973b; Galdikas 1985b; Schürmann and van Hooff 1986). Even though all males are seen to mate (Galdikas 1978; Mitani 1985b; Utami *et al.* 2002) they apparently differ in their timing relative to conception, and in the Sumatran sites subordinate flanged males do not seem to be successful at all (this chapter; van Schaik 2004).

The reproductive success of flanged males is made possible by the females' preference. The dominant flanged male in an area may be able to exclude other flanged males from his immediate ranging area, but he certainly does not exclude all unflanged males. Also, a dominant flanged male cannot prevent unflanged males from forming consortships with females in the same area. However, his dominant position allows him to maintain a consort, whereas unflanged males may be forced by bigger males to give up a consort.

The picture that emerges from these data indicates an interaction between the three components of sexual selection. Male-male competition is intense, in particular among flanged males. Females prefer mating with the dominant flanged male, who is therefore likely to have the highest siring success in the local population. They have an aversion to mating with unflanged males, especially when they are receptive, who must therefore resort to coercion and have a lower per capita

mating success than the dominant flanged male. Thus, female preferences set the scene for the male-male competition; if they had no preferences at all, unflanged males would be much more successful than flanged males due to their higher mobility. At least in Sumatra, other flanged males achieve very few matings, and almost certainly sire very few offspring. Whether this is also true for Borneo needs to be assessed in future work.

16.4.2 Male bimaturism

Utami *et al.* (2002) discussed (and reject) two previously untested hypotheses, advanced to explain male reproductive behavior and bimaturism in *Pongo* sp., and proposed a third hypothesis. The 'range-guardian' hypothesis (MacKinnon 1974) asserts that the flanged males are post-reproductive and defend a range in which they tolerate sexually active unflanged male relatives. This hypothesis could be rejected because the unflanged males are not clearly related to the dominant flanged male, and the latter sires offspring. The 'female choice' hypothesis asserts that flanged males tolerate unflanged males in their range because they rely on female preference to favour flanged males. However, unflanged males also sire offspring, and all males compete heavily for access to females. Utami *et al.*'s (2002) preferred hypothesis was that the two male morphs represent coexisting alternative male reproductive strategies, 'sitting, calling, and waiting' for flanged males versus 'going, searching, and finding' for unflanged males. While clearly consistent with the known data on mating behavior, this idea leaves unexplained why unflanged males may remain unflanged for so long.

The evolutionary strategy of delayed maturation could then be understood in two ways. One possibility is that the timing of the switch is due to frequency-dependent benefits. Then the two strategies would be alternatives yielding equal reproductive success in an equilibrium situation (Galdikas 1985b; Maggioncalda *et al.* 1999; Utami *et al.* 2002; Utami Atmoko and van Hooff 2004; Knott and Kahlenberg 2007). However, current data suggest that unflanged males can sire offspring,

but mainly with females not (yet) effectively mate-guarded by flanged males, for example because of their unpredictable fertility (nulliparous females). Thus, if the new interpretation of the Ketambe data holds (and if the observational estimates from most other orangutan observers are correct), unflanged males have lower per capita success than the dominant flanged male, but higher success than the other flanged males. Paternity data from more sites and of larger samples are needed to assess the difference in reproductive success within and between the two male morphs, but at our present state of knowledge the morphs do not seem to yield equal reproductive success.

A second possibility is that the phenomenon of developmental arrest represents a 'waiting room strategy' in which unflanged males bide their time until they can assume, without too much risk, the highly contested role of flanged male (Schürmann and van Hooff 1986; van Hooff 1995). In the meantime they can make the best of a poor job by engaging in sexual interactions, even though this offers only limited reproductive success. This idea leaves out one critical issue, however: most flanged males are spectacularly unsuccessful at achieving matings. To deal with this omission, van Schaik (2004) argued that a flanged male who is not dominant over other flanged males in the same area is worse off than an unflanged male in acquiring matings. The large flanged males have high costs of locomotion and maintenance and cannot indefinitely maintain a consortship when the female does not cooperate, as she does with a preferred male. If such males give long calls to attract females they run a high risk of a confrontation with a more dominant flanged male. Unflanged males travel faster and roam more widely (see Chapter 18), and can also endure longer associations (*e.g.* Wich *et al.* 2006b). They are therefore better able to gain some potentially fertile copulations through chance encounters with fertile females and by closely following consort pairs and engaging in sneak matings. Thus, only when a male is likely to achieve dominance in an area would the mating benefits of SSCs outweigh its costs. It is possible that a male may need to wait for a long time for such an opportunity to arise, which would explain the developmental arrest.

16.4.3 Island differences

Much of the above account is based on intensive observations at Ketambe with additional data collected at Suaq, whereas the data from the Bornean sites is still less detailed. It is possible that some aspects of sexual behavior and male mating strategies differ between Sumatra and Borneo, and perhaps even within islands. A first indication for this is the observed difference in local ratios of flanged to unflanged males between Sumatra and Borneo (Delgado and van Schaik 2000): for every flanged male observed at Suaq or Ketambe, there are about two unflanged males, whereas for all known Bornean sites the opposite holds, showing roughly two known flanged males for each known unflanged male. This observation suggests that developmental arrest is certainly more prominent among Sumatran orangutans, and perhaps even limited to them. One possible explanation for this is that dominant Sumatran flanged males may be more effective at mate guarding than their Bornean counterparts because they can afford to maintain longer consortships (Delgado and van Schaik 2000). Thus non-dominant Sumatran flanged males are at a disadvantage compared to more agile unflanged males in acquiring matings. However, if Bornean flanged males cannot maintain long consortships, other flanged males could sire offspring as well at any given time at a particular site, whereas unflanged males will be virtually excluded (except from nulliparous females). More work is needed to establish any firm island differences, but on current information some meaningful differences are to be expected.

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