



A Comparison of Female Mating Strategies in *Pan troglodytes* and *Pongo* spp.

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Abstract Orangutans and chimpanzees differ in many aspects of their mating and social systems. Nevertheless, because both great apes require enormous maternal investment in offspring and because female reproductive potential is limited, female orangutans and chimpanzees should be selective of their mates, yet expected to exhibit anti-infanticide strategies such as mating with multiple males. We review and compare mating patterns in orangutans and chimpanzees to understand how these critical pressures are filtered through the different demands of the socioecology of each species. We highlight the variation in female mating behavior as a function of the proximity of ovulation. We conclude that both genera pursue tactics for paternity confusion by mating with multiple males and by mating cooperatively or even proceptively with nonpreferred partners when conception is unlikely. Mating selectivity is suggested by variation in proceptive behavior toward particular partners and by increased resistance of nonpreferred partners during the periovulatory period. Thus, data for both species support a mixed mating strategy whereby females shift their mating behavior in accordance with ovulatory status to accommodate the competing demands of mate selectivity and paternity confusion.

Keywords Chimpanzees · orangutans · reproductive strategies · female mate choice

Introduction

Ape life histories place a premium on reproductive success, particularly for females. For example, ape female physiology appears to be particularly well adapted to allow

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reproduction selectively under favorable ecological conditions (Emery Thompson and Wrangham 2008a, b; Knott 2001, 2005). Ape female behavioral strategies are also expected to have undergone selection to increase offspring survivorship. Elucidating female strategies in apes is particularly difficult in light of complex mating dynamics and the influence of male competition, body-size dimorphism, and coercion. We review the mating behavior of orangutans (*Pongo* sp.) and chimpanzee (*Pan troglodytes*), with the goal of understanding how female strategies for mate selection and paternity confusion compare in 2 great apes with contrasting socioecologies.

Chimpanzees and orangutans share many ecological, behavioral, and life historical characteristics. Both are large-bodied, frugivorous, male-dominant hominoids with relatively slow life histories. However, despite the similarities, their social and mating systems are clearly distinct. Whereas chimpanzees are more gregarious and frequently travel, socialize, and forage in multimale, multifemale groups (Nishida 1968; Sugiyama 1968), orangutans are generally dispersed and much more solitary (Galdikas 1979; Rijksen 1978; van Schaik and van Hooff 1996). Orangutans are substantially more sexually dimorphic than chimpanzees (Leigh and Shea 1995), and males are characterized by 2 adult morphs (Kingsley 1982; Maggioncalda *et al.* 1999; Crofoot and Knott *in press*). Flanged males are considerably larger than unflanged males and exhibit well-developed cheek flanges, throat pouches, and long hair (Delgado and van Schaik 2000; Knott and Kahlenberg 2007). Unflanged males have limited secondary sexual development, though they are sexually mature (Utami *et al.* 2002; Crofoot and Knott *in press*). Female orangutans may encounter both resident and transient males (Mackinnon 1974, 1979; Singleton and van Schaik 2002). Individual flanged males long call regularly (Delgado 2006) and compete intensely to exclude other flanged males from their ranges, whereas unflanged males often associate with one another (Utami *et al.* 2002). By contrast, adult male chimpanzees are highly gregarious and cooperatively defend their home ranges from outside males (Goodall 1986; Mitani and Watts 2005).

Orangutan and chimpanzee females share many similarities in their reproductive biology. Orangutan menstrual cycles are somewhat shorter than those of chimpanzees (28 vs. 35 days: Knott 2005; Markham 1990; Stumpf 2007; Wallis 1997), but share a similar hormonal profile that contrasts in important ways from those of nonhominoids (Bentley 1999; Czekala *et al.* 1988). In both species, females are sexually receptive outside of the periovulatory period; thus sexual behavior is not strictly controlled by hormonal fluctuations (Dixson 1998). These 2 ape genera have the slowest reproductive schedules of any nonhuman primate, reaching maturity at *ca.* 10 yrs, experiencing a 1–4-year period of adolescent subfecundity, and experiencing interbirth intervals that are at the extreme range for all mammals (orangutans: 6–10 yr, Knott 2001; Wich *et al.* 2004; chimpanzees: 5–7 yr, Emery Thompson *et al.* 2007; Stumpf 2007). Both typically experience several cycles before conception and conceive primarily during periods of high energy availability (Emery Thompson and Wrangham 2008a, b; Knott 1999, 2001). One major difference in their reproductive biology is that cyclic changes in estrogens produce a large, pink perineal swelling in chimpanzees (Nadler *et al.* 1985), whereas there is no

morphological indicator of sexual receptivity in orangutans (Galdikas 1981; Graham-Jones and Hill 1962).

In spite of their socioecological differences, we expect females of both taxa to be under similar selective pressures in their reproductive behavior. First, according to sexual selection theory, females are predicted to select high-quality mates. Females may select mates that can provide higher-quality genes or protection for mother and infant, thereby enhancing offspring survival and reproductive potential (Andersson 1994; Clutton-Brock 1998; Maynard Smith 1991). Though occurring widely across animal species, direct or indirect female choice may be particularly critical where female reproductive potential is most limited because of long-term investment in each offspring. Second, infanticide risk should also play a significant role in determining female mating behavior, and should select for anti-infanticide strategies, such as paternity confusion by mating with many males (Hrdy 1981). Infanticide risk is predicted to be high for both species, due to shared factors such as long interbirth intervals, low female reproductive potential and, in particular, a high lactation-to-gestation ratio. The latter is thought to be one of the best predictors of infanticide risk (van Schaik 2000). Researchers have reported infanticide in chimpanzees multiple times across long-term field sites (Wilson and Wrangham 2003). There are no reports of infanticide among wild orangutans. However, because infanticide among chimpanzees was not observed until many years of intense study, increased observation time may permit its detection in orangutans. The semi-solitary nature of orangutans may increase the potential risk of infanticide, but such low interaction rates also limit the occasions when opportunistic infanticide could occur and be observed.

In sum, despite substantial differences in their social and mating systems, both great apes are expected to exhibit female mate selectivity and infanticide counterstrategies such as paternity confusion. Though these appear to be competing aims, ape female sexual behavior may allow their dual expression. In particular, female behavior during the periovulatory period (POP) should be oriented toward conception, e.g. with a preferred male, while behavior outside of POP may reflect other strategies. We emphasize that accurate interpretation of the mating strategies of chimpanzees and orangutans requires knowledge of their likelihood of conception, which is possible only with the combination of behavioral and endocrinological information.

Chimpanzees have an extended sexually active phase averaging 10–12 d (Tutin and McGinnis 1981), which is marked by a prominent sexual swelling. The sexually active phase consists of 2 parts: the POP, lasting 3–5 d, during which conception is most likely to occur, preceded by a lengthier nonperiovulatory phase (non-POP), during which the sexual skin is fully tumescent but conception is unlikely (Emery Thompson 2005; Stumpf and Boesch 2005). Thus, sexual swellings in chimpanzees attract multiple mates with a probabilistic indicator of ovulation while potentially obscuring the most profitable time for mating (Nunn 1999). Chimpanzee males allocate mating effort in relation to sexual swelling and female fecundity (Deschner *et al.* 2004; Emery Thompson 2005; Emery Thompson and Wrangham 2008a). Orangutan females display no visual signal of receptivity such as a sexual swelling, and orangutan males initiate copulations at all times of the cycle (Fox 1998; Nadler 1982, 1988). However, female behavior, such as actively seeking flanged males, facilitating intromission, or initiating sexual behavior is likely to be important for

selectively cuing males to conceptive periods (Fox 1998; Schürmann 1982; Bosch Van der Werff ten 1982). In both apes, there are 2 types of copulations: those in which females willingly engage and those in which females show resistance (Galdikas 1985a, b; MacKinnon 1974; Mitani 1985; Stumpf and Boesch 2005, 2006a), though, particularly in orangutans, some matings may involve both cooperative and resistant behaviors (Knott *in press*; Knott *et al.* 2007; Fox 1998). If females of both genera attempt to influence paternity, they should try to mate most selectively during the POP. Specifically, both are predicted to increase resistance to nonpreferred males during POP. Likewise, if females attempt to confuse paternity and face relatively low costs of mating, they should increase proceptivity and decrease resistance rates to nonpreferred males when conception is unlikely.

Methods

We review female orangutan and chimpanzee mating behavior to incorporate the considerable diversity in behavioral findings across study sites. First, we compare general features of sexual behavior in the 2 species: frequency and duration of copulation, frequency of forcible copulation attempts by males; and rates of female proceptive, prosexual, and resistant behavior. Next, we ask whether a female's sexual behavior is affected by her conception likelihood (POP vs. non-POP) or by variation in mate preference. Finally, we look at the interaction of the 2 factors: whether female conception likelihood influences proceptive or resistant behavior toward particular males or male morphs. Appropriate testing of our hypotheses depends on the detailed quantification of female sexual behaviors and hormonal status, rarely analyzed in the same study. Thus, to understand the complex relationship between fecundity, copulatory frequency, and partner preference, we review the existing literature on sexual behavior in the species and draw particularly from our own studies of the relationship between ovulatory timing and mating behavior in each (Emery Thompson and Wrangham 2008a, b; Stumpf and Boesch 2005, 2006a, b; Knott *et al.* 2007). In assembling the available data, we were cognizant that study methods vary, that definitions for one species may not easily apply to the another, and that there is likely to be additional meaningful variation across populations of the same species. A discussion of the methods and data considerations for quantifying mating behavior and ovulatory status follows.

Defining Female Sexual Behavior

Mating represents a compromise of the interests of both males and females; thus copulation data alone are insufficient to explain female reproductive strategies. Instead, detailed observations of female behavior before, during, and after a sexual interaction are necessary.

In both chimpanzees and orangutans, sexual interactions can be initiated by either males or females. Males initiate copulation through a variety of solicitation behaviors such as display of the erect penis (Galdikas 1985a; Goodall 1986; Nadler 1982). In chimpanzees, females typically initiate copulations by approaching the male and presenting their sexual swelling; in orangutans, females may present their

genitalia. Copulation initiation provides one mechanism to evaluate their partner preferences (Galdikas 1981; Stumpf and Boesch 2005; Wallis 1992). Female proceptivity is thus defined as female-initiated sexual behavior toward a male, with no preceding male sexual invitation. Orangutans, in particular, also engage in other proceptive sexual behaviors during mating, such as a female facilitating intromission via insertion of the male's penis into her vagina, oral stimulation of the male's penis, and a female allowing male manual and oral stimulation of her genitalia. The behaviors may occur in both male- and female-initiated sexual interactions. Thus, to facilitate comparisons with chimpanzees, we use the term prosexual to distinguish positive female sexual response—regardless of which sex initiated the sexual interaction—from proceptivity, i.e., strictly female-initiated sexual behavior.

Female mate preferences can also be assessed via quantification of female initial response to male mating attempts, independent of the outcome of the interaction (Stumpf and Boesch 2005). Female chimpanzees respond to male solicitations in 2 ways: by cooperating (rapidly approaching the soliciting male and presenting for copulation; Tutin 1979), or resisting his solicitation. Female resistance does not imply that copulation did not occur. Female resistance may also occur with or without male coercive behavior. The success of female resistance is difficult to compare directly in the 2 genera, largely because their sexual interactions are quite different; thus, it is difficult to use an operationalized definition of resistance that is standard for both great apes. For chimpanzees, males frequently signal sexual interest from some distance and rarely, if ever, manhandle or position females for mating (Tutin 1979). Female chimpanzee resistance consists of ignoring the solicitation, avoiding the male, screaming, attacking, or attempting to leave (Tutin 1979; Stumpf and Boesch 2005). Orangutan studies have focused on quantifying physical resistance once a male has made contact with a female in an attempt to mate (Fox 1998; Mitani 1985). Researchers have thus operationalized female resistance in orangutans as active resistance, screaming, struggling, wrestling, and escape behavior (Fox 1998; Galdikas 1985a, b, c; Mitani 1985). Other less obvious form of resistance such as avoidance and threat vocalizations have occurred in orangutans, but this is not yet rigorously quantified.

Male and female chimpanzees are in frequent association, making it feasible to analyze data on a female's relative proceptivity and resistance rates toward a particular male vs. her average for all males (Stumpf and Boesch 2005). However, among orangutans, far rarer mating behavior and infrequent association between the sexes generally preclude comparable analyses of female preferences for particular males. It is possible, though, to evaluate female responses to the 2 morphs of males, flanged and unflanged, during periods in which conception likelihood is high or low. Based on variation in female proceptive and receptive behavior (Fox 1998; Knott *in press*; Knott *et al.* 2007) and substantial evidence from previous studies (Fox 1998; Galdikas 1985a, b, 1995; Schürmann and van Hooff 1986; Utami 2000), flanged males are preferred to unflanged males.

Determining Reproductive Phase

To understand how reproductive status influences sexual interactions, it is essential to assess female fertile periods accurately. Researchers have commonly used

inference based on behavior or swelling stage, bringing with it considerable sources of potential error. For example, because orangutans lack external signs of cycling stage, the age of dependent offspring can provide one measure of the likelihood that a female is experiencing sexual cycles. However, because of variation in the length of postpartum amenorrhea (Knott 2001), one cannot use the age of the youngest offspring to pinpoint resumption of ovarian cycles. Only mothers of young infants can be assumed not to be ovulating. Though proceptive behavior by captive female orangutans follows a cyclic pattern (Nadler 1982, 1988), using this criterion for defining cycle phase is clearly circular. Thus, in both species, ovulatory timing must be assessed with care, and hormonal methods should be used if possible.

Hormonal determination of ovulation can be accomplished via 2 methods: ovulatory test sticks or ovarian hormone quantification. Where daily urine collection is possible, ovulation test kits, i.e., dipsticks that detect the high levels of luteinizing hormone characteristic of impending ovulation, such as the Ovquick test (Quidel, San Diego, CA), can reliably indicate reproductive status and timing of ovulation in apes (Czekala *et al.* 1987; Knott 1996; Stumpf and Boesch 2005). One can also derive ovulation time from hormonal profiles through measuring ovarian hormones (estrogen and progesterone) or their metabolites noninvasively via urine or feces (Emery Thompson 2005; Fox 1998; Knott 1998, 2005; Knott *et al.* 2007). Great ape hormonal profiles are characterized by a preovulatory peak in estrogen levels and a postovulatory sustained increase in both estrogen and progesterone levels (Bentley 1999; Czekala *et al.* 1988). Thus, ovulation should occur reliably between the estrogen and progesterone peaks (Hodges *et al.* 1986; McArthur *et al.* 1981; Nadler *et al.* 1985). Given relatively frequent sampling of both hormones, trained researchers can define a probable ovulatory window (Hodges *et al.* 1986; Fig. 1).

The limited time during which copulation can lead to conception is dependent on sperm and extrafollicular egg viability (France 1981; Gomendio and Roldan 1993). Studies of fertility patterns in apes and humans suggest that most pregnancies result from copulations 1–3 d before and including ovulation (Elder and Yerkes 1936; France *et al.* 1992; Wilcox *et al.* 1995); thus we define POP as occurring 3 d before and including ovulation.

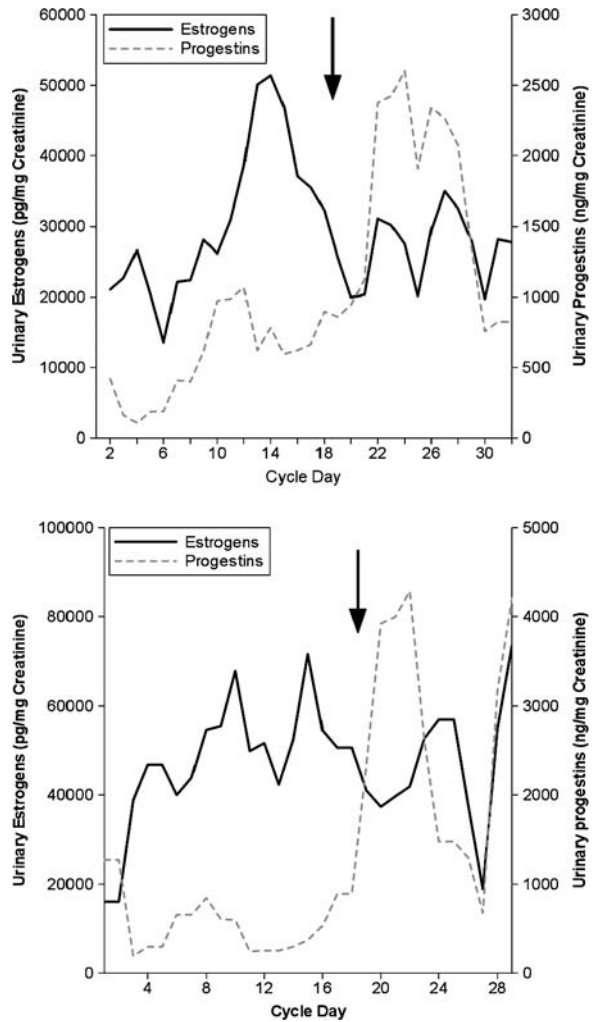
Both chimpanzees and orangutans copulate during pregnancy (Wallis 1992; Knott *et al.* 2007). Thus, hormonal testing is also useful to establish that conception has occurred, and is accomplished via hormonal assays, or the use of pregnancy kits that test for the hormone human chorionic gonadotropin (hCG). Though designed for humans, test kits such as QuickVue (Quidel, San Diego, CA; Knott, 1997) and Aimstick (Craig Medical, Vista, CA; Emery Thompson 2005) have proven effective for diagnosing early pregnancy in apes.

Results

How Does Copulatory Behavior Vary Between Chimpanzee and Orangutan Females?

While both chimpanzee and orangutan females mate with multiple males, copulation rates differ dramatically. Copulation rates for chimpanzees range from 0.3 to 4.9

Fig. 1 Ovarian hormone dynamics (3-d moving averages) in 2 sample cycles for chimpanzees (**a**, data from Emery Thompson 2005) and orangutans (**b**, data from Knott *et al.* 2007), demonstrating the hormonal transitions typical of ovulatory cycles in both genera. In both cases, ovulation would have occurred on *ca.* d 18 (arrow), after the early cycle peak in estrogen levels and before the marked increase in progesterone levels.



copulations per observation hour, and vary by individual female attractiveness and study population (Table I). Orangutans mate much less frequently, from 0.002 to 0.14 copulations per observation hour. Conversely, chimpanzee copulations last only 7 s on average, while orangutan copulations last *ca.* 8–10 min (Table I).

Orangutans and chimpanzees differ substantially in proceptivity rates (Fig. 2a,b; Table I). At all sites, chimpanzee females initiated about one-quarter of all copulations. However, the outcome of female proceptivity varied widely across sites. Female proceptivity in Tai was much more effective (77%) than that recorded in Gombe by Wallis (1992), who found that only 40% of female-initiated sexual interactions were successful. At Mahale, Matsumoto-Oda (1999) also found that the majority of female attempts at courtship in chimpanzees were unsuccessful. At Tai, Stumpf and Boesch (2006a) found that female proceptivity and resistance rates

Table I A comparison of chimpanzee and orangutan reproductive parameters at different sites

Species	Study population	Copulation frequency ^a	Copulation duration	Female proceptivity (%) ^b	Forced copulation (%) ^c
<i>Pan troglodytes</i>	Gombe	0.5–3.5/h ¹	7s ¹³		0.002 ²⁴
	Budongo	0.4–1.3/h ²			
	Kanyawara	0.4–0.9/h ^{2,3}	7s ¹⁴	27 ³	
	Ngogo	2.5–4.9/h ⁴			
	Mahale	0.5–1.0/h ⁵	7s ¹⁵	21 ¹⁷	
	Kalinzu	2.2–3.2/h ⁶		29 ⁶	
	Tai	0.3/h ⁷	7s ⁷	24 ¹⁸	0.001 ¹⁸
<i>Pongo pygmaeus</i>	Gunung Palung	0.002/h	477s ¹⁶	21 UF; 21 F ¹⁶	21 UF ¹⁶ ; 42 F ¹⁶
	Kutai	0.05–0.1/h ⁹		<1 ⁹	95 UF; 46 F ⁹
	Tanjung Puting	0.008/h ¹⁰	648s ¹⁰	<1 ²²	86 UF ²² 3 F ¹⁰
<i>Pongo abelii</i>	Ketambe	0.02/h ¹¹		0 UF; 53 F ²⁰	41 UF; 2 F ^{20, 23, 19}
	Suaq Balimbing	0.02/h ¹²		1 UF; 97 F ¹²	57 UF; 0 F ²¹

^a Ranges from published studies may reflect variation across females, from POP to non-POP, or from non-conception to conception cycles.

^b Percentage of copulations initiated by females. UF = unflanged males, F = flanged males.

^c Female resistance is defined here as the percentage of sexual interactions that females attempt to resist that result in copulation.

¹ Wallis 2002; ² Emery Thompson 2005; ³ Emery Thompson and Wrangham 2008a, b; ⁴ Watts 2007; ⁵ Takahata *et al.* 1996; ⁶ Furuichi and Hashimoto 2002; Hashimoto and Furuichi 2006; ⁷ Stumpf and Boesch 2006a; ⁸ Knott *et al.* 2007; ⁹ Mitani 1985; ¹⁰ Galdikas 1981; ¹¹ Utami and van Hooff 2004; ¹² Fox 1998; ¹³ Tutin and McGinnis 1981; ¹⁴ Emery Thompson and Wrangham, unpublished data; ¹⁵ Nishida 1997; ¹⁶ Knott *et al.* 2007; ¹⁷ Matsumoto-Oda 1999; ¹⁸ Stumpf and Boesch 2006a (data reflect % of sexual interactions); ¹⁹ Knott and Kahlenberg 2007; ²⁰ Schürmann and van Hooff 1986; ²¹ Fox 2002; ²² Galdikas 1985a, b, c; ²³ Utami 2000; ²⁴ Goodall 1986.

correlate with male mating success in the periovulatory period, suggesting that female preferences can be exerted. In contrast to chimpanzees, orangutan female proceptivity, defined here as female sexual initiation, is very variable (Table I). At some sites, almost no female proceptivity, occurred, especially toward unflanged

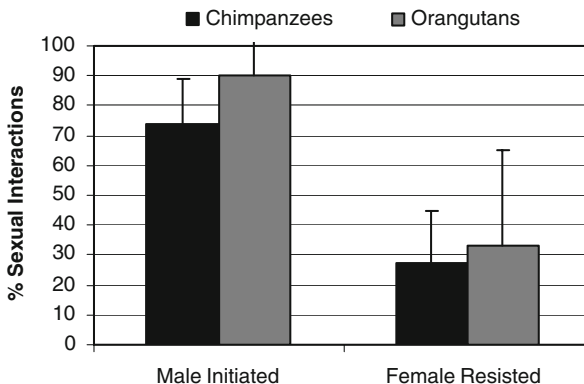


Fig. 2 Initiation of sexual behavior and success of female solicitations in (a) Tai chimpanzees (Stumpf and Boesch 2006a) and (b) Gunung Palung orangutans (Knott *et al.* 2007). Female chimpanzees initiated *ca.* one-fourth of sexual interactions and attempted to resist *ca.* one-third of male solicitations. Almost all orangutan sexual interactions were male-initiated. Orangutan females, like chimpanzees, resisted *ca.* one-third of male solicitations.

males. However, orangutan females can exhibit high rates of proceptivity toward flanged males, as reported at Suaq Balimbing for adult females by Fox (1998, 2002) and at 2 other sites for adolescent females by Galdikas (1979, 1981) and Schürmann (1982) and Schürmann and van Hooff (1986: Table I). Among both orangutans and chimpanzees, adolescent females are often particularly proceptive (Pusey 1978a, b; Schürmann and van Hooff 1986). Thus, orangutan mean proceptivity rates appear to be lower overall than in chimpanzees, though at least some orangutan females are highly proceptive toward particular partners or when young.

Female chimpanzees and orangutans differ substantially in their expression of prosexual behavior. Orangutan females often play an active prosexual role during mating, aiding with intromission, manually or orally stimulating the male, and facilitating pelvic thrusting (Fox 1998; Galdikas 1979, 1981; Knott and Kahlenberg 2007; Utami Atmoko 2000). Though female chimpanzees perform solicitation displays (Nishida 1997), initiate intromission (Tutin 1979), or manually stimulate male genitalia before mating (R. Stumpf, *unpub. data*), active female sexual behavior during intromission is considerably more limited in chimpanzees, perhaps owing to the very brief duration of mating, their dorsoventral copulatory position, and the possibility that extended sexual behavior may incite aggression from competing males toward either partner.

Both female chimpanzees and orangutans attempt to resist some proportion of copulations. Female Tai chimpanzees attempted to resist *ca.* 28% of male solicitations, and successfully avoided unwanted copulations in the majority of cases (69%: Stumpf and Boesch 2006a). Forced copulations are exceptionally rare in chimpanzees (<0.01%; Table I), though males use other coercive tactics in mating contexts, such as herding, harassing and intimidating females (Muller *et al.* 2007; Stumpf and Boesch 2006a, b). In orangutans, Fox (2002) reported that Suaq females resisted 36% of male mating attempts, which is similar to the 30% resistance rate observed at Gunung Palung (Knott *et al.* 2007). Forced copulations are considerably more common in orangutans, occurring with both flanged and unflanged males (Table I). Unlike chimpanzees, orangutan female resistance rarely prevents mating once physical contact has been established (Fox 1998; Galdikas 1985a), though the differing operational definitions of resistance for each genus preclude direct comparison. At Kutai, females were able to struggle free in only 7–8% of forced mating attempts (Mitani 1985) similar to Gunung Palung (Knott *et al.* 2007).

Do Females Express Proceptivity, Prosexuality and Resistance Differently Toward Different Males?

In chimpanzees, researchers have examined variability in female sexual behavior in relation to individual partner identity as well as age and dominance rank. Mating studies at Tai (Stumpf and Boesch 2005) and Kanyawara (Pieta 2008) showed significant variation among dyads in proceptivity and resistance rates. At Tai, female proceptivity rates varied with the relationship between male and female rank such that low-ranking females were more proceptive to low-ranking males and high-ranking females were more proceptive to high-ranking males (Stumpf and Boesch 2005). This finding is supported at Kanyawara, where nulliparous females, which tend to be low-ranking, were significantly more likely to initiate copulations with

low-ranking males (Emery Thompson and Wrangham 2006). Parous Kanyawara females copulated with higher-ranking males, though they initiated a relatively small proportion of the copulations (Emery Thompson and Wrangham 2006; Muller *et al.* 2006). Prosexual behavior in chimpanzees appears to be extremely rare.

In orangutans, researchers have typically examined variability in proceptivity, prosexuality, and resistance in light of male developmental status: flanged or unflanged. The majority of orangutan mating studies have shown markedly greater proceptivity rates toward flanged vs. unflanged males; in the exception (Kutai: Mitani 1985), females were not proceptive to either type of male (Table 1). Researchers have quantified prosexuality only for Gunung Palung (Knott *et al.* 2007), where females are more prosexual toward flanged, prime males during their POP. Overall rates of female prosexuality were highest during pregnancy.

However, there is a high degree of variability in mating resistance vs. cooperation toward both flanged and unflanged males (Knott *in press*). At 2 of 5 sites, females were resistant to flanged males *ca.* 50% of the time, vs. <5% resistance at the other 3 sites. Similarly, cooperative mating with unflanged males varied between 5% and 79% at the 5 sites. Thus, male type alone does not in itself predict female sexual behavior across sites (Knott *et al.* 2007). Male rank and residence status may also be important (Fox 2002; Galdikas and Wood 1990; Schürmann 1982; Knott *in press*), though researchers have not examined them well given the scarcity of matings. Interpopulation differences in female behavior may also reflect variation in the number of males (Knott *in press*); e.g., the study with the highest rates of proceptivity and lowest resistance to flanged males had mating data for 1 resident and 1 nonresident flanged male (Fox 1998).

Does the Interaction Between Female Reproductive State and Male Traits Influence Female Sexuality?

Because females face conflicting demands of paternity confusion and mate selectivity, we predicted that females would alter their behavior toward particular males depending on ovulatory status. The hypothesis is supported in both chimpanzees and orangutans. At Taï, Stumpf and Boesch (2005) found that female resistance and proceptivity toward particular males depended on female likelihood of conception. They designated preferred and eschewed partners for each female according to her proceptivity and resistance rates to each male relative to all other males. Females were significantly less proceptive to eschewed males during POP than in non-POP, and significantly more resistant to eschewed males during POP than in non-POP (Fig. 3). For preferred males, there was no difference in proceptivity or resistance between POP and non-POP. Via similar methods, Pieta (2008) also found shifts in female proceptivity and resistance toward particular males at Kanyawara depending on fecundity. Females were more proceptive and less resistant to preferred males in the POP relative to the non-POP. In contrast, females showed a trend toward less resistance and more proceptivity to eschewed partners in non-POP relative to POP. Thus, both studies suggest that female mating behaviors toward particular males shift according to ovulatory status.

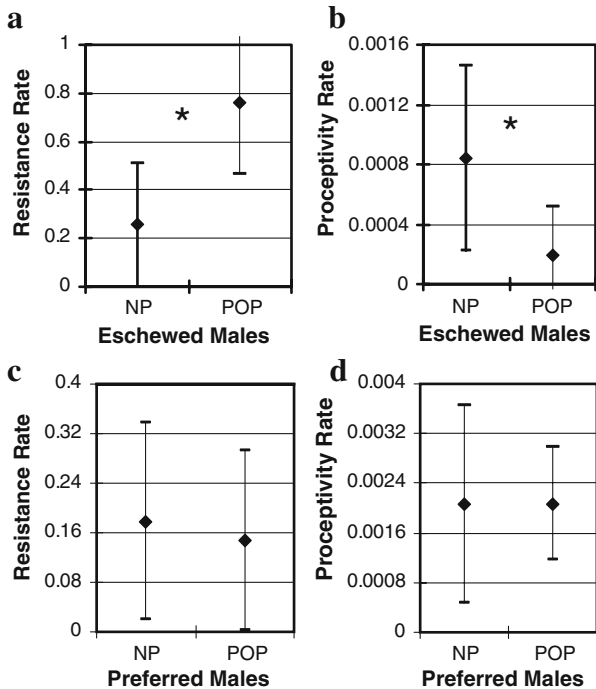
Our study of mating behavior and endocrinology in orangutans tested the predictions of the mixed strategy hypothesis, by examining female mating behavior in the POP and

non-POP phases (Knott *et al.* 2007). An important predictor of female resistance was the interaction between endocrine status and male type (Knott *et al.* 2007). Results were dramatic, indicating that all matings during POP (determined by endocrinological data) were with flanged males. The majority (75%) were with prime males, and past-prime males accounted for the remainder. In contrast, the further females were from their conceptive period the more matings that took place with nonprime males. The closer females were to ovulation, the more resistant they were to mating with unflanged or past-prime males. Further, females showed the least resistance and highest rates of proceptivity and prosexuality, during early pregnancy, before a pregnancy swelling was present, which in our view is evidence of a mixed strategy in orangutans that helps explain much of the variability in female mating behavior and response.

Discussion

We compared patterns of female sexual behavior and mate choice in chimpanzees and orangutans. In addition, we examined the hypothesis that in both chimpanzees and orangutans, females shift their mating behavior according to conception risk to achieve the dual goals of paternity confusion and mate selectivity. Females of both great apes exhibited a mixed mating strategy, though they differed in their expression.

Fig. 3 Differences in average chimpanzee female resistance and proceptivity rates toward non-preferred (eschewed) (a, b) and preferred males (c, d), respectively, depending on likelihood of conception. Resistance rates were significantly higher in the periovulatory period (POP) than in the non-periovulatory period (NP) toward eschewed males (a), while proceptivity rates were significantly higher in NP than in POP toward eschewed males (b). Females were not consistent in their pattern of resistance and proceptivity toward preferred males across phases (c, d). (Modified from Stumpf and Boesch 2005). Data are from Tai National Park.



The differences in chimpanzee and orangutan female sexual behavior and physiology are likely due to socioecological differences. Chimpanzees live in large, stable multimale, multifemale communities that form temporary subgroups of varying composition throughout the day (Goodall 1986). Orangutans live at low population densities and are largely solitary (Knott and Kahlenberg 2007); thus male-female encounter rates, at most sites, are very low vs. those of chimpanzees. Differences in social systems may influence differences in mating, proceptivity, prosexuality, resistance, and forced copulation rates.

For example, chimpanzee interpopulation variation in copulation frequency has been associated with the number of potential male partners, supporting a role for multiple mating in paternity confusion (Watts 2007). Thus, it is conceivable that orangutan copulation rates are lower simply because the number of partners contacted is much lower and that the low copulation rates are sufficient to confuse paternity. The dramatic difference in the length of mating (7 s vs. 8–10 min; Table I) seems likely due to the differences in community structure as well. Chimpanzee males must quickly mate to avoid being displaced, whereas orangutan males are less constrained by direct mating interference, though it sometimes occurs. Why orangutans mate so long, though, is difficult to explain. The period of active intromission in orangutans is extraordinary vs. that of other apes (Dixson 1998), which may be important in understanding orangutan resistance.

Female chimpanzees and orangutans use different strategies to attract male attention. Chimpanzee females have evolved a large sexual swelling to attract male interest, whereas orangutan females have not. The lack of a visual signal, i.e. estrous swelling, in orangutan females suggests that males have little knowledge of the conceptive period, and flanged males may rely on female behavior and association patterns as indicators of fertility (Schürmann and van Hooff 1986). Whereas chimpanzees use proceptivity to initiate copulations, orangutan females, in contrast, are generally less proceptive, i.e., solicit a smaller proportion of matings than do males. However, one of the most striking differences between the 2 apes is the high degree of prosexuality in orangutans vs. chimpanzees. Prosexuality occurred primarily under 3 contexts: toward flanged males while ovulating, toward all males during the early part of pregnancy and by adolescent females. Thus, females may use prosexual behavior to influence male mating behavior (Fox 1998; Schürmann 1982). Females became more prosexual toward nonpreferred males (unflanged and past-prime) the further they were from conception; thus, we argue that they are using this sexual behavior to entice male interest during these nonfecund periods as a paternity confusion strategy (Knott *et al.* 2007). Females may need to signal fecundity to flanged males because flanged males occasionally show disinterest in mating (Schürmann 1982; Schürmann and van Hooff 1986), and, because at times they mate with multiple females on the same day, sperm depletion may be an issue. We suggest that like female proceptivity in chimpanzees, prosexual behavior in orangutans can be both an honest and dishonest indicator of fecundity. During the POP, males may accurately use it as a sign of female fecundity. However, the high degree of prosexuality during early pregnancy is not an honest signal of fecundity. The most likely explanation for postconception mating is paternity confusion as a deterrent to infanticide (Knott *et al.* 2007). van Noordwijk and van Schaik's (2000) analysis of reproductive behavior across mammals supports this hypothesis with

their finding that only anti-infanticide can explain the pattern of postconception mating.

Both chimpanzee and orangutan females show variation in association patterns corresponding to reproductive status and likelihood of conception. Female chimpanzees associate more frequently with males when they have a sexual swelling, than during nonswelling phases (Goodall 1986). Growing evidence suggests that female orangutans respond to and travel toward flanged male long calls (Utami and Setia 1995; Galdikas 1981; Fox 2002; Delgado 2006; Mitra Setia and van Schaik 2007). It has been demonstrated in captivity that female orangutans in control of male access approach and solicit a caged mate selectively with regard to phase in menstrual cycle (Nadler 1995; Maple *et al.* 1979). Thus, female orangutans may exert mate preferences by initiating associations with preferred males when they are most fecund (Fox 2002). Utami and van Hooft (2004) have argued that flanged orangutan males adopt a sit-call-and-wait reproductive tactic that may provide an important mechanism for female orangutans to influence mating patterns, particularly in light of the relative ineffectiveness of female resistance once a male physically attempts to mate. Mate guarding may prevent unflanged males from gaining access to females during the POP (e.g. Fox 2002). Due to the dispersed nature of the orangutan social system, association patterns and who is responsible for dyad formation is presently not well understood. Thus, future research on orangutan reproductive strategies might focus on determining which sex is responsible for approaching the other and how consortships are formed, particularly in relation to female reproductive status, and whether ranging patterns may also reflect avoidance of particular males.

Chimpanzee and orangutan females avoid mating with some males, particularly during their POP. In chimpanzees, females were highly resistant and non-proceptive to non-preferred males during the POP (Fig. 3). In the study of Knott *et al.* (2007), females mated only with flanged males during the POP. However, we hypothesize that when nonpreferred males attempt matings during the POP, females highly resist them. The most violently resisted mating during our study was with a past-prime male during the female's POP (Knott *et al.* 2007). Female orangutans are usually unable to prevent copulation with nonpreferred males once physical contact has been established, which is unsurprising given the differences in orangutan sexual dimorphism and the social context of mating. However, while resistance is not very effective in thwarting copulation attempts in orangutans, it may have other important effects such as reducing the duration of intromission and preventing ejaculation (Fox 1998, 2002; Knott *et al.* 2007). Orangutan females may also resist or avoid male sexual interest in subtle ways not yet operationalized. For example, Fox (2002) found that females sometimes formed nonmating temporary parties with flanged males apparently to escape the attention of unflanged males. In her study, females in consortship with flanged males resisted copulations with unflanged males significantly more successfully than unaccompanied females did because they either fled to the flanged males for protection, or because the flanged males chased away the unflanged males when the female struggled and vocalized (Fox 2002).

The selective use of proceptivity, prosexuality, and resistance by female chimpanzees and orangutans supports the hypothesis that both genera employ a mixed strategy of paternity concentration and confusion. Both chimpanzee and orangutan females mate with several males when cycling, but both shift their

selectivity in accordance with conception risk. Both great apes exhibit cooperative, proceptive, or prosexual behavior toward nonpreferred partners during nonconceptive periods. These patterns of behaviors are not consistent with female active or cryptic choice of sire, nor with ensuring fertilization. Instead, females concentrate and show mating patterns consistent with an aim to confuse paternity. These patterns were striking enough to emerge even within a small sample of orangutan matings (Knott *et al.* 2007) and in spite of the very promiscuous sexual activity of chimpanzees. It is also intriguing that these similarities exist even though there is an obvious difference in sexual advertisement between the taxa. Though the sexual swelling in chimpanzees limits mating activity to a more restricted time period than concealed ovulation in orangutans, females still mate when conception is highly unlikely (Emery Thompson 2005), and they appear to use the time to copulate with nonpreferred males (Stumpf and Boesch 2005). The results are consistent with a more generalized female strategy to increase paternity confusion when there is a low risk of conception and to deflect nonpreferred male solicitations at ovulation to prevent males from siring offspring.

We encountered potentially confounding elements in comparing data from different field studies. One potential complication in assessing proceptivity and resistance rates within a taxon is the ratio of adult/adolescent males or females and flanged/unflanged males included in the data. For example, in one orangutan study, 52% of matings occurred within 1 dyad, and adolescent females accounted for 96% of all observed matings (Schürmann and van Hooff 1986). Adolescent females chimpanzees and orangutans, often exhibit distinctly different sexual behavior from that of adult females (Emery Thompson and Wrangham 2008a, b; Fox 1998; Galdikas 1981; Schürmann and van Hooff 1986), making it difficult to generalize results from adolescents to all females. In addition, the proportion of adolescents vs. adults or developmental class, e.g. unflanged or flanged, of the males varies considerably across studies (Matsumoto-Oda 1999; Mitani 1985). If females encounter a larger proportion of nonpreferred mates, overall rates of resistance may be higher. Likewise female proceptivity may be low at sites where there are few matings with flanged males. This sampling issues are difficult to overcome, particularly in studies of orangutans, because copulation frequencies are low enough to preclude dyadic analysis, especially when a proportion of individuals are transient.

Other sources of variation include the observer's targeted sex. Some studies target males (Mitani 1985; Schürmann and van Hooff 1986), whereas others target females (Knott *et al.* 2007; Stumpf and Boesch 2005). Proceptivity and resistance rates based on studies that target males will likely differ substantially from proceptivity and resistance rates based on studies targeting females. In orangutans, if samples include more unflanged males, resistance and forced copulation rates may be much higher than in studies targeting adult females. Hence data based on female targets may be preferable in studies that attempt to understand and to compare female reproductive strategies, and vice versa for males.

Additional differences in recorded proceptivity or resistance rates within and between taxa may be due to varying operational definitions of the behaviors. For example, researchers have quantified orangutan female resistance as an active struggle against a male's attempts to position her sexually. However, females may

resist male sexual advances in several additional ways, such as running away from or deterring male advances before active sexual positioning, and these resistance tactics may indicate that female ability to resist mating is underestimated and merits further attention. In addition, authors differ in whether they label positive female sexual behavior that occurs after male initiation as proceptivity or they limit the operational definition of female proceptivity to sexual initiation. We label the former as prosexuality to distinguish it from proceptivity, defined as strict female sexual initiation (e.g. Stumpf and Boesch 2005, 2006a). Moreover, because of the lengthy duration of orangutan mating, female sexual response may vary from resistant to proceptive and vice versa within the same sexual interaction, depending on male coercion, a third party or other factors (Fox 1998; Galdikas 1981; Rijksen 1978; Knott *in press*). Thus, explicit definitions of particular measurements and the use of standardized operational measures, e.g., for proceptivity and resistance, are needed to compare intraspecific variation in reproductive behavior among sites and between taxa.

We focus on female mating behaviors and the strategies females employ in their attempts to achieve reproductive success. The behavior occurs in complex mating systems in which male preferences and mating competition also play an important role in influencing overall mating patterns. Because of male dominance to females among both chimpanzees and orangutans, males may attempt to intimidate females directly through aggressive acts (Muller *et al.* 2007; Stumpf and Boesch 2006a, b), or indirectly through their larger body size, and such real or perceived threats may change female behavior in ways that are difficult to measure. For instance, females may be more likely to resist other mating partners when in the presence of a high-ranking male, regardless of their own preferences, or behave more cooperatively with large or aggressive males because resistance may not be successful (cf. Stumpf and Boesch 2006a). Similarly, a female's response to a male may be informed by her previous interactions with him. The efficacy of intimidation and consequences for mating success in chimpanzees differ across sites (Stumpf and Boesch 2005, 2006a, b; Muller *et al.* 2007) and may vary depending on subspecies, socioecology, demography, or individual variation (Stumpf 2007). Thus, it is important to acknowledge the interaction between female and male strategies in determining mating outcomes. However, our goal was to examine whether similar selective pressures on these apes have resulted in similar female reproductive strategies. We suggest that females of both genera use a mixed strategy to attempt to achieve their own reproductive objectives, though female orangutans and chimpanzees differ in how they implement them.

Conclusion

Results from our comparative study suggest that similar selective pressures on females in differing social and ecological environments lead to differing tactics to achieve the same reproductive goals. The analyses also emphasize the importance of comparative studies for understanding the evolution of primate mating systems and female sexual strategies. By incorporating hormonal information and disentangling female behavior in potentially conceptive and nonconceptive matings, we can begin

to understand the diversity of tactics and unifying elements of female reproductive strategies in chimpanzees and orangutans.

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