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Orangutans: Sexual Coercion without Sexual Violence

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It is perhaps not surprising, given the prevalence of male aggression against women in humans, that the role of sexual coercion as a male mating strategy in animals emerged into the mainstream academic consciousness after the women's movement of the 1970s. With the publication of Smuts and Smuts's seminal paper on the subject in 1993, the importance of sexual coercion as a form of sexual selection was proposed, and sexual coercion has received increasing, though still somewhat limited, attention from scientists. Clutton-Brock and Parker (1995) extended the argument of sexual coercion as sexual selection by proposing a theoretical framework consisting of three male coercive strategies: forced copulation, harassment, and intimidation. These two reviews, as well as subsequent research, have highlighted the conditions under which sexual coercion is manifested in primates. However, one question that has received little or no attention is what causes differences in the *degree of force* used during sexual coercion. That subject is explored here through an examination of forced copulations in orangutans.

Orangutans are unusual among the primates, and indeed among mammals, for their use of force during copulation. At some orangutan sites a majority of copulations are forced. Therefore, orangutans apparently represent one of the most extreme cases of sexual coercion in the animal kingdom. Particularly because of presumed parallels between orangutan forced copulations and human rape, this behavior has been viewed as one of the most violent expressions of coercive male behavior. Smuts and Smuts (1993), for example, detail the prevalence of sexual coercion in the primate literature, concluding that "the most dramatic examples of apparent sexual coercion come from wild orangutans" (p. 6). However, perhaps counterintuitively, despite the high rates of forced copulation in orangutans and the often prolonged struggle of females, severe wounding of females has never been reported (MacKinnon 1974; Rijksen 1978; Schurmann 1981, 1982; Galdikas 1981, 1985a, b; Mitani 1985a; Schurmann and van Hooff 1986; Fox 1998; Utami 2000). In fact, Galdikas (1981:289) reports that "as soon as raping males stopped thrusting, they invariably released the female. Nor did any female sustain injuries or wounds as a result of rape." Thus, I argue here that orangutan males use force as a way to accomplish copulation but do not intentionally wound females. Orangutan coercive sexual behavior is direct coercion and is not used as an indirect means to influence or control future female sexual behavior, as seen in species such as chimpanzees and humans.

In this chapter, I explore orangutan sexual coercion through four objectives. First, I review the evidence of sexual coercion in orangutans and highlight the actual diversity in expression of this behavior exhibited between populations. I argue that copulations can rarely be classified as either forced or consensual because most mating involves elements of both proceptivity and resistance. I also demonstrate that factors other than male morphotype (flanged versus unflanged), such as female hormonal status, contribute to the frequency of forced copulation, and I present a number of hypotheses to be tested. Second, I argue that orangutan sexual coercion may be driven by females resisting males in order to avoid the energetic and disease costs of multiple matings, as well as the cost of insemination by a genetically inferior male. Females may benefit from resisting because it decreases the total length of the mating; sometimes it may also prevent ejaculation and may garner support from the dominant male. Third, I highlight the finding that, although copulations are often forced in orangutans, the degree of physical *wounding* is extremely low. In particular, I evaluate the degree of force associated with orangutan sexual coercion in the light of comparative data from chimpanzees and humans. Finally, I discuss how measures of the *degree of physical force* used in coercion may help us distinguish between direct and indirect coercion and the motivations behind that coercion, and I present further hypotheses for investigation.

Forced Copulations

Defining Forced Copulation in Orangutans

Forced copulations have been described by all orangutan researchers, starting with the earliest pioneers (MacKinnon 1974; Galdikas 1978; Rijksen 1978; Galdikas

1979, 1981; Schurmann 1981, 1982; Mitani 1985a; Schurmann and van Hooff 1986). Galdikas (1981:288) provides the first operational definition: "Rape occurred when a male attempted to copulate or copulated with a female who resisted his efforts to position her for intromission. A female's struggles ranged in intensity and duration all the way from brief tussles with squalling and some pushing and slapping at the male's hand to protracted violent fights in which the female struggled through the length of the copulation, emitted loud rape-grunts and bit the male whenever she could."

Despite the ubiquitous observation of forced copulations, most orangutan researchers report that some copulations are ambiguous and cannot be easily designated as either forced or cooperative (Rijksen 1978; Galdikas 1981; Fox 2002; Knott et al. in review). Often a copulation can have elements of both male force and female proceptivity and can switch from being cooperative to resistant or resistant to cooperative. For example, at Gunung Palung we have seen females that run away, screaming from a male, are chased and then grabbed by him but then become very proactive during the copulation, sitting on top of the male and facilitating intromission and copulatory thrusting. Fox (1998), working at Suaq in Sumatra, reports a number of matings that began cooperatively but eventually turned coercive, as females struggled to escape. For example, she described the mating of the adult female "Ani" with an unflanged male. The mating began with the female showing no resistance and continuing to feed on fruit that was within her reach. After three minutes the male grabbed her feeding hand in an attempt to reposition her. This was followed by 12 minutes of struggle, which included the male biting and hitting the female until he achieved ejaculation.

Despite this frequent mix of coercive and cooperative elements, orangutan copulations are usually characterized as either forced or consensual based on an overall impression of male actions and female responses. This subjective dichotomization masks some of the interesting variation in mating behavior that may help us better understand its origin. In the next sections, I discuss the factors, based on earlier studies as well as a reexamination of the literature and our more recent detailed analysis (Knott et al. in review), that determine whether a copulation is categorized as forced, consensual, or ambiguous. Following Clutton-Brock and Parker (1995), I first consider forced copulations, then harassment, and finally intimidation and nonmating aggression.

Flanged vs. Unflanged Males

Orangutan males are commonly divided into two distinct morphological forms based on the presence or absence of protruding cheek flanges. Flanged males who sport these prominent, fibrous protrusions are very large, typically weighing over 80 kg in the wild (Markham and Groves 1990, Figure 4.1a). They give loud bellowing long calls audible for up to 800 m in the forest (Mitani 1985b) that are used to advertise their presence to other flanged males and perhaps to females (Knott and Kahlenberg 2007). In contrast, unflanged males are smaller, do not give long calls, do not have cheek flanges (Knott and Kahlenberg 2007, Figure 4.1b), and are subordinate to flanged males. Flanged males are almost entirely solitary, except when consorting with females, and show absolute intolerance of other flanged males. Unflanged males commonly travel in small bands and normally are not aggressive toward other males (Knott and Kahlenberg 2007). Physiologically, both male morphs are sexually mature, as evidenced by their ability to father offspring and their similar levels of follicle-stimulating hormone (FSH)—responsible for viable sperm production (Maggioncalda et al. 1999). Testosterone levels are lower in unflanged males in both the wild (Knott in prep) and captivity (Maggioncalda et al. 1999, 2000), accounting for the lack of secondary sexual characteristics in the unflanged males. This condition of male bimaturism is extremely rare in mammals, with perhaps the possible other exception of mandrills (Atmoko and van Hooff 2004).

The developmental status of the male is the key variable that has been investigated in relation to forced copulation. Forced copulation is often depicted as the typical mating strategy of unflanged males, whereas matings with flanged males are said to be consensual (Rijksen 1978; Galdikas 1979, 1981; Schurmann 1982; Fox 2002). However, the data show much more variability than is commonly appreciated (Mitani 1985a). Figure 4.2 distinguishes forced versus consensual copulations according to male "type." At some sites, such as Suaq, all of the copulations with flanged males were consensual, whereas at Kutai and Gunung Palung, approximately 50% of flanged copulations were forced. The data for unflanged males are similar. At Gunung Palung, Kutai, and Suaq a significant proportion of copulations with unflanged males were consensual. Thus, flanged status of the male alone is not sufficient to explain the majority of orangutan mating data.

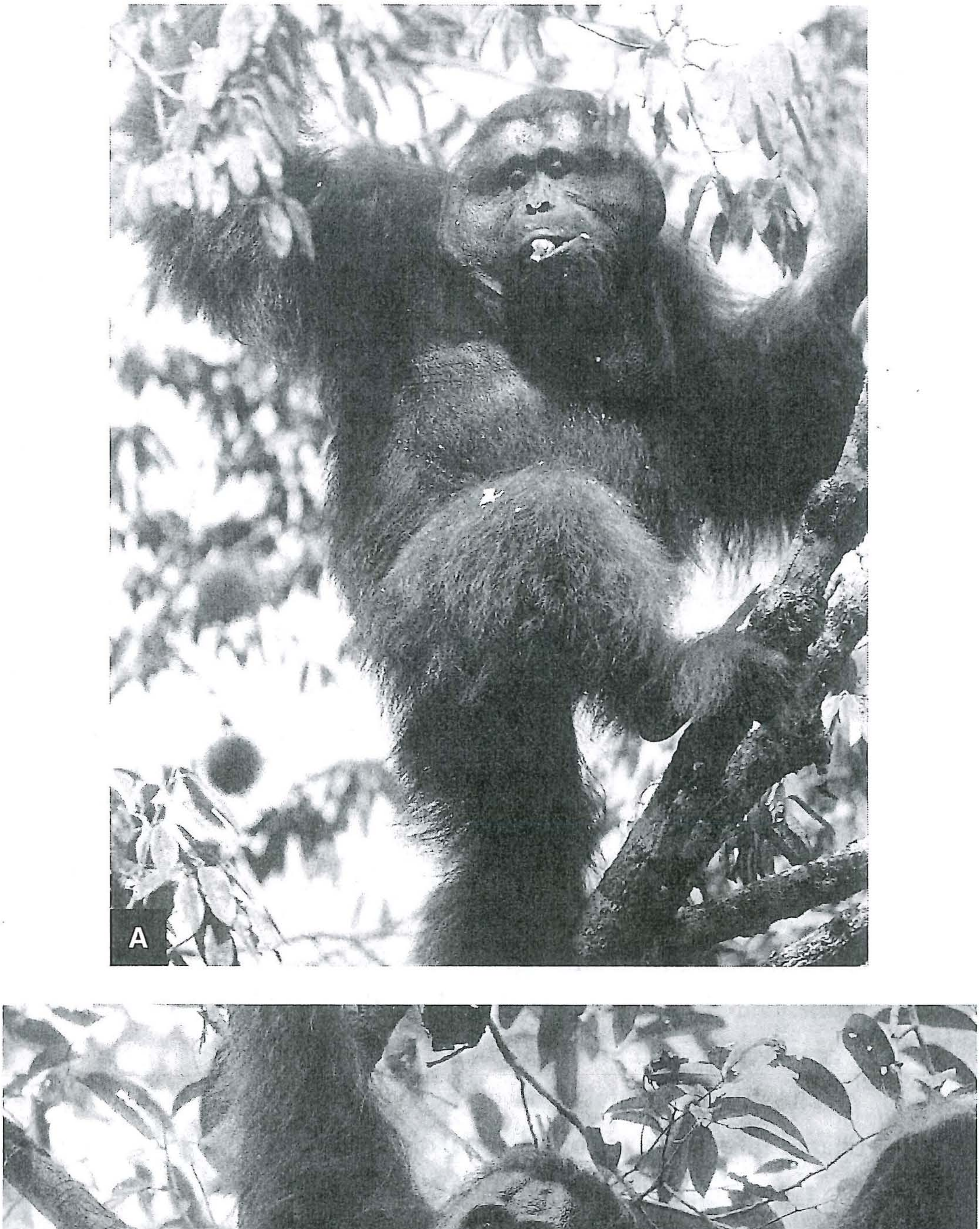

Figure 4.1 Photos of a (a) flanged and (b) unflanged male from Gunung Palung National Park. Photos by Tim Laman.

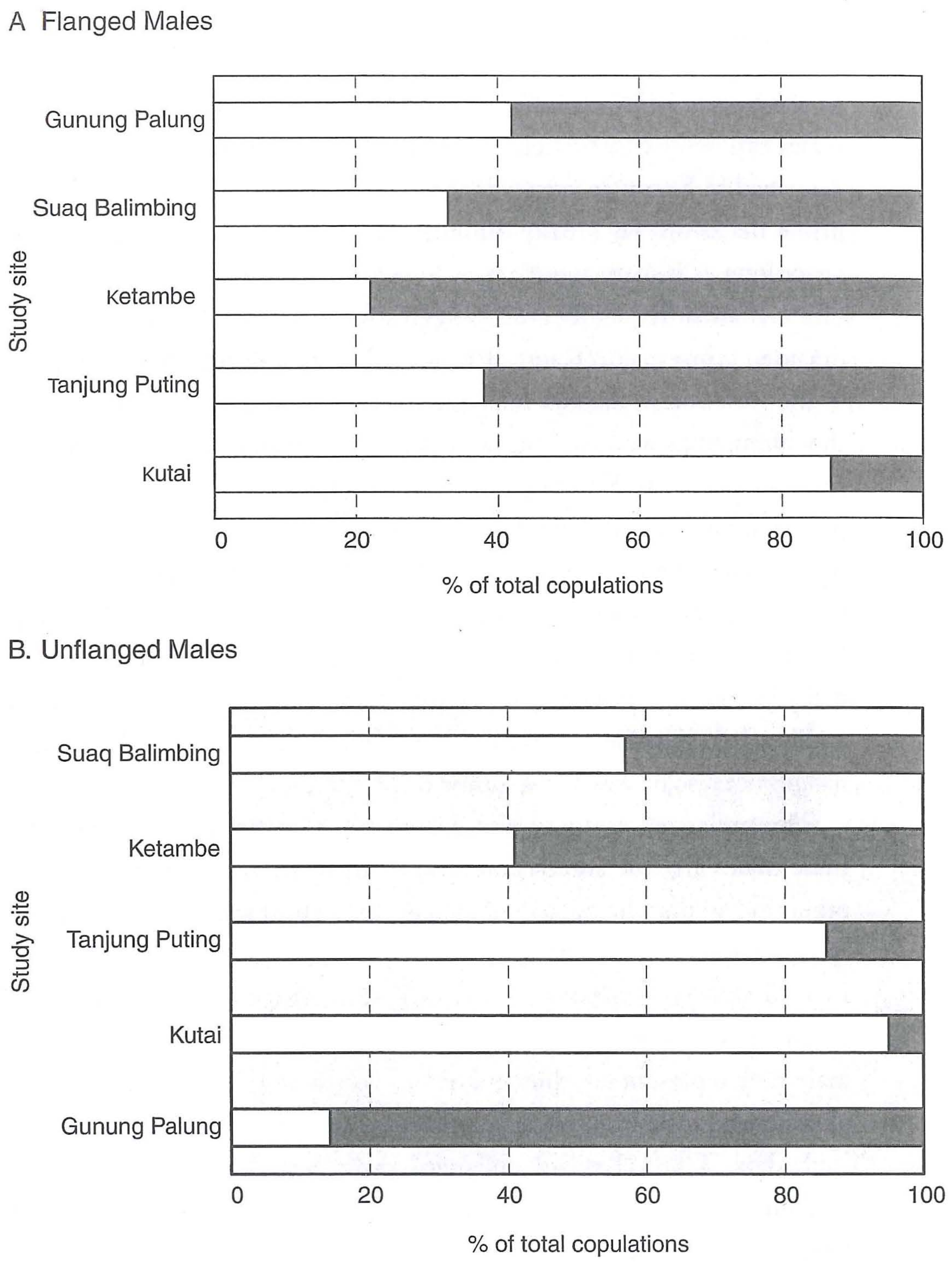

Figure 4.2 Forced (white bars) and cooperative (black bars) copulations involving (A) flanged and (B) unflanged orangutan males at five study sites. Sample sizes are for copulations of known outcome and are as follows (unflanged/flanged): Suaq Balimbing (N=90/66): Fox, 2002; Ketambe (N=38/50, 94/70; averaged between two studies): Schürmann and van Hooff 1986, Utami Atmoko 2000; Tanjung Puting (N=22/30): Galdikas 1985a, b; Kutai (N=151/28): Mitani 1985a; Gunung Palung (N=24/19): Knott et al. (in review).

Male Status

In addition to being classified as flanged or unflanged, within these categories males can be further broken down by other aspects of their status or rank. As described in Knott (in prep), flanged males may be prime or past prime. Past-prime males display greatly diminished cheek flanges, they give significantly fewer long calls, have significantly lower testosterone levels and energy expenditure, mate infrequently, are less aggressive toward other males, and are subordinate to prime males (Knott, in review). This new distinction may explain some of the variation in flanged male matings. For example, at Gunung Palung, although matings with past-prime males were rare, females showed high levels of resistance to them (Knott et al. in review). This was particularly true during the periovulatory period. Females were also significantly less proceptive to past-prime males than to prime males (Knott et al. in prep). At Kutai, where the highest percentage of forced copulations by flanged males has been reported, Mitani (1985a) found that 62% of these flanged forced copulations were by one male that had the least developed cheek flanges. He was never seen to mate non-forcibly. It is possible that rather than being young, this male had small cheek flanges because he was a past-prime male.

The unflanged category also encompasses several types of male. Some of these males are true adolescents whose cheek flanges have not yet developed, others are adults who have remained in this status for many years, and still others are in the process of developing cheek flanges (Crofoot and Knott in press). In wild study populations, many of these unflanged males are unhabituated, transients who briefly visit study areas. Their ages and the "type" of unflanged male they represent are thus unknown. To females, however, these three types of unflanged male likely elicit very different responses to mating attempts. In her study, Fox (1998) classified unflanged males into three size categories (small, medium, and large) and found that mating behavior differed significantly between the categories. Females may be able to recognize males who are on the verge of becoming flanged. At Ketambe, the consensual matings with an unflanged male observed by Utami Atmoko (2000) were with a male who developed cheek flanges and displaced the dominant male six months after these matings were observed. In fact, this male achieved a majority of the copulations attributed to unflanged males, and 50% of paternity at this site was attributed to him (Utami 2002).

Residential Status

Orangutan males range over large areas, and residential status may heavily influence female preference. Mitani (1985a) found that 90% of matings by the dominant flanged male were consensual, whereas only 34% of the matings by the other six nonresident flanged males were. Similarly, Fox (1998, 2002) describes a strong female preference for the resident flanged male, and Utami Atmoko (2000) describes how females that normally preferred the dominant flanged male copulated cooperatively with lower ranked flanged males and unflanged males during periods of male rank instability. At Gunung Palung, among flanged males, the dominant prime flanged male received the majority of the copulations over nonresident flanged males. Thus, residential status and male rank, within a given male "type," is an important determinant of female choice.

Female Reproductive and Ovarian Status

In orangutans, the periovulatory period (POP) when conception occurs cannot be distinguished visually because of the lack of a sexual swelling. Thus, hormonal analysis must be used to determine a female's ovulatory status. At Gunung Palung we (Knott et al. in review) have shown that female ovulatory status interacts with male type to influence whether the copulation is forced. Copulations near or during the POP were almost exclusively with flanged prime males (Figure 4.3) and all copulations with flanged males during the POP were cooperative (Figure 4.4). As a female's fecundity decreased, unflanged males were more likely to mate successfully. Adult females during the POP were significantly more attractive to males than were non-POP or pregnant females. Interestingly, this is not just a reaction to female proceptivity, as the most proceptive females were those in the early stages of pregnancy. All copulations with females during early pregnancy were cooperative.

Copulatory Sequence

Mitani (1985a) suggested that the first encounter between a male and female often leads to a forced copulation, but subsequent copulations are more likely to be consensual. He found this pattern in three of five associations. At Gunung Palung, we only found this pattern in one out of ten such associations (Knott et al. in review). Consecutive copulations on the same day included every possible pattern: cooperative:cooperative, cooperative:forced, forced:forced, and

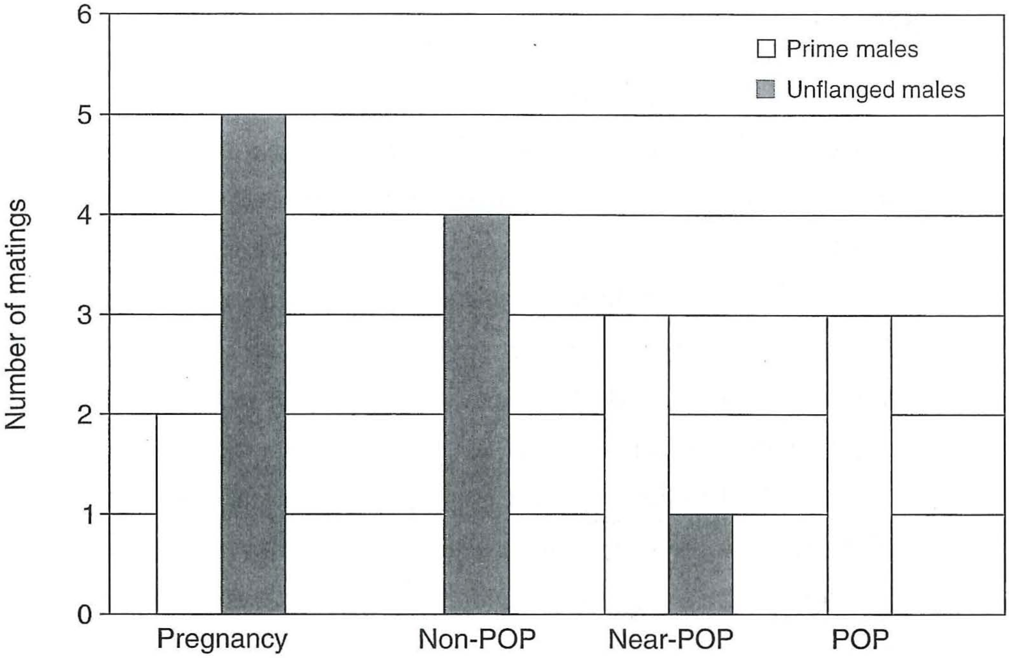

Figure 4.3 Male type during matings of known female ovulatory status.

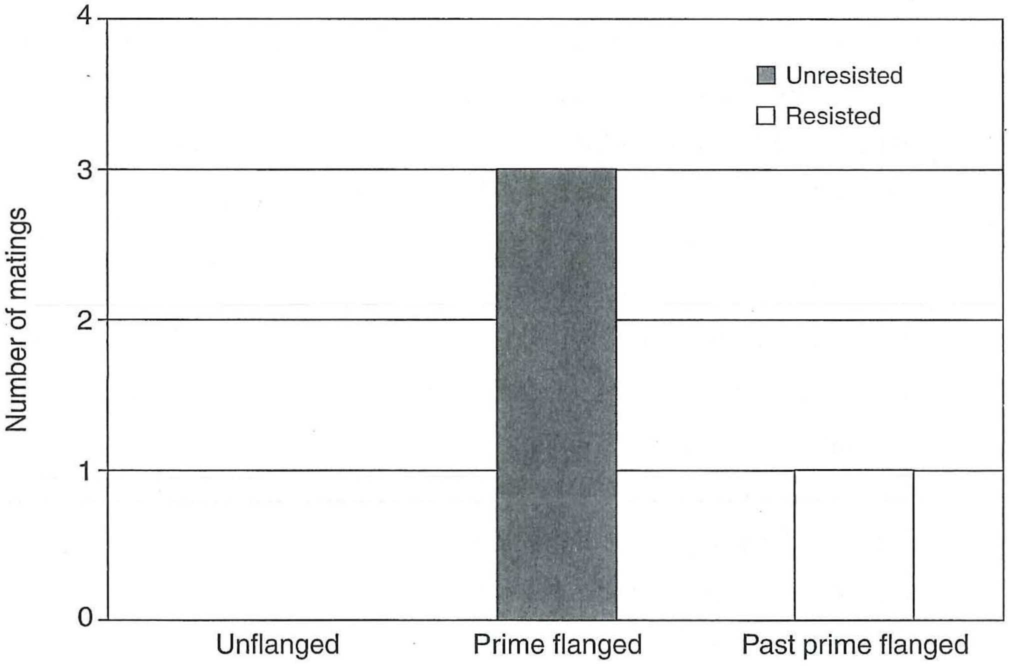

Figure 4.4 Male type and resistance of matings during the periovulatory period (POP).

forced:cooperative. In one such instance of sequential matings at Gunung Palung, a prime flanged male forced a female that was traveling with an unflanged male to copulate despite her very active resistance throughout the mating. Soon after, they mated again, and the female offered no resistance whatsoever. In another case, an unflanged male mated with another adult female, and the first copulation involved genital inspection by the male and no resistance by the female. After three hours they mated again. This time the female ran away, and the male had to force her legs apart to mate with her. Likewise, during the course of these long matings, copulations can switch from forced to consensual and vice versa (average eight minutes of copulatory thrusting for matings at Gunung Palung). Whether the female in these situations eventually accepts the male, gives up, was just "testing" him, or simply has changed her mind is unclear. It may be that during the mating, or between consecutive matings, females are reassessing the relative costs of resisting vs. acquiescing, and behaving accordingly. Thus, in Fox's (1998) description of a female who resisted after initially cooperating, the cost of the mating changed when she was prevented from continuing to eat.

Male:Female Ratio and Number of Copulations

In orangutans, the adult sex ratio in a study area is expected to vary with the availability of fecund females, which itself is related to female energetic status influenced by food availability (Knott 1998a, 2001; Knott et al. 2009). Indeed, both Kutai and Gunung Palung report periods when there were several fecund females simultaneously and a concurrent large increase in the number of males using the study site. As the operational sex ratio increases, I would predict more male-male competition for fecund females and an increase in the number of forced copulations. This relationship has been demonstrated in insects and birds; as the male to female ratio increases, males become more likely to force females to mate (Low 2005).

To test for a relationship in orangutans between the ratio of males to females and the number of forced copulations, I examined data from the literature from the five study sites where this information is available. I found that the ratio of males to females was a significant predictor of the degree of female resistance ($p<0.01$, Pearson correlation$=0.957$) for both flanged and unflanged males. Indeed, there was a significant correlation between forced matings by flanged males vs. forced matings by unflanged males ($p<0.005$, Pearson correlation$=0.982$). There was no relationship between the rate of consensual copulations and the male:female ratio ($p=0.624$, Pearson correlation$=-0.300$). I would predict, based on the endocrine data cited above, that these forced matings are occurring at different times in the females' cycle depending on male type. Thus, whereas normally a flanged male may be able to "sit and wait" for ovulating females to come to him, with increased male competition he may become more likely to try and mate with a non-POP female who, because of her ovulatory status, resists him, resulting in a forced copulation. Similarly, with a high operational sex ratio it may be increasingly difficult for flanged males to prevent unflanged males from mating with females during the POP. Thus, there may be more successful matings of unflanged males during the POP, which I would predict should be noncooperative because ovulating females show a clear preference for flanged males.

Female Strategies

Intriguingly, the relationship between increased male density and increased female resistance in orangutans is opposite of that found in some insects and birds, where the term *convenience polyandry* has been used to describe why a female may resist some matings and acquiesce for others. Convenience polyandry occurs when a female mates because the cost of acquiescing is less than the benefits she would gain by resisting or escaping that mating. Factors involved in the assessment of this cost-benefit analysis include risk of mortality, predation, disease transmission, loss of feeding opportunities, and the impact of fertilization. For both damselflies (Rivera and Andres 2002) and New Zealand stitchbirds (Low 2005), the operational sex ratio as it relates to the number of mating attempts is an important factor in determining female mating decisions. In these species, however, females resist matings below a certain threshold, but, as the rate of male harassment increases beyond that threshold, females acquiesce and mate with nonpreferred males in order to reduce the cumulative costs of mating. For females below the threshold, resisting the occasional mating is less costly than mating. When harassment by nonpreferred males is infrequent, females resist the matings, but as mating attempts increase, the costs of resisting becomes too great and females acquiesce. The opposite is true for orangutans because as the number of mating attempts increases, the level of female resistance increases. Although the risks of mortality and predation are not applicable in the case of the orangutan, disease transmission, loss of feeding opportunities, and the impact of fertilization by a nonpreferred male are all potential risks a female assumes during a mating. Thus, increased female resistance in response to an increased number of mating attempts is not explained by convenience polyandry, but may be observed because the benefits of escaping or trying to escape still outweigh the costs of mating for orangutans.

Another argument for female resistance is provided by van Schaik (2004), who argues that females resist matings with nonpreferred males in order to attract the attention of the dominant flanged male and to let him know that she is mating unwillingly. If the dominant male is nearby, he may be able to intervene in the mating. However, because of the dispersed ranging behavior of orangutans, the female is likely to be too far away from the dominant male for him to either hear or assist her. Van Schaik (2004) argues that a responding male may initiate a consortship with the female or assess that she was not ovulating. However, she may indeed be ovulating, and it would seem a better strategy to *not* attract the attention of the dominant male so as not to decrease his paternity certainty. The ability of a dominant male to be aware of matings by females with other males, and to intervene in these matings, likely varies depending on orangutan density.

Why do females mate with nonpreferred males at all? The endocrinological data from Gunung Palung are intriguing because they suggest that the least fecundable females, those during the non-POP, are the most likely to mate with unflanged males. Pregnant females exhibited the most proceptive behavior toward all male types. One interpretation of this behavior is that females are using a paternity confusion strategy to avoid the possibility of infanticide from these males (Hrdy 1981; van Schaik et al. 1999; Knott et al. in review). It may benefit a female to occasionally mate cooperatively with nonpreferred males in the population in order to confuse paternity and avoid potential infanticide. This interpretation is problematic; although orangutans are predicted to be vulnerable to infanticide (van Schaik and Kappeler 1997), thus far it has never been observed (Delgado and van Schaik 2000). However, other evidence is suggestive of this strategy as well. Utami Atmoko's (2000) observation at Ketambe that when the dominant male was being challenged females were much more likely to copulate with otherwise nonpreferred males (subdominant flanged males, unflanged males, and stranger males) and that there was a highly significant increase in matings with pregnant females during this period is also consistent with an anti-infanticide interpretation. Furthermore, Delgado (2003) in playback experiments showed that females ignored the long calls of resident flanged males, but that females and their infants became very upset when long calls of stranger males were played and they often fled in the opposite direction.

Temporal Variation in Fruit Availability and Its Effects on Female Fecundity

The copulatory rate at Gunung Palung is associated with increased food availability, increased caloric intake, and consequently positive female energetic status (Knott 1999; Knott et al. 2009). In turn, positive female energy balance is significantly correlated with higher estrogen production and thus higher fecundability. Thus, because of the long interbirth interval in orangutans of seven to nine years (Galdikas and Wood 1990; Knott 2001; Wich et al. 2004) and the frequent clumping of conception years (Singleton and van Schaik 2002), the number of fecund females using a given study area is likely to vary considerably. Thus copulation rates and rates of sexual coercion may fluctuate substantially between study periods. In Borneo, where fruit availability varies dramatically, the rate of copulations may be explicitly tied to varying fruit production, and thus study periods may show pronounced variation in the number of copulations.

Therefore, another interesting distinction between study sites is the number of copulations witnessed per observation hour (Figure 4.5). Gunung Palung stands out as having a very low copulatory rate compared to Kutai with a very high rate. Mitani (1985a) points to the availability of three fecund females during his study at Kutai where he witnessed 179 copulations in 3600 observation hours. By contrast, Rodman (1977), also working in Kutai, witnessed only two copulations in 1644 observation hours. At Gunung Palung 28% of our total matings were observed during a three-month mast period of high fruit availability, representing just 4% of our total sampling time. In most months no matings were observed,

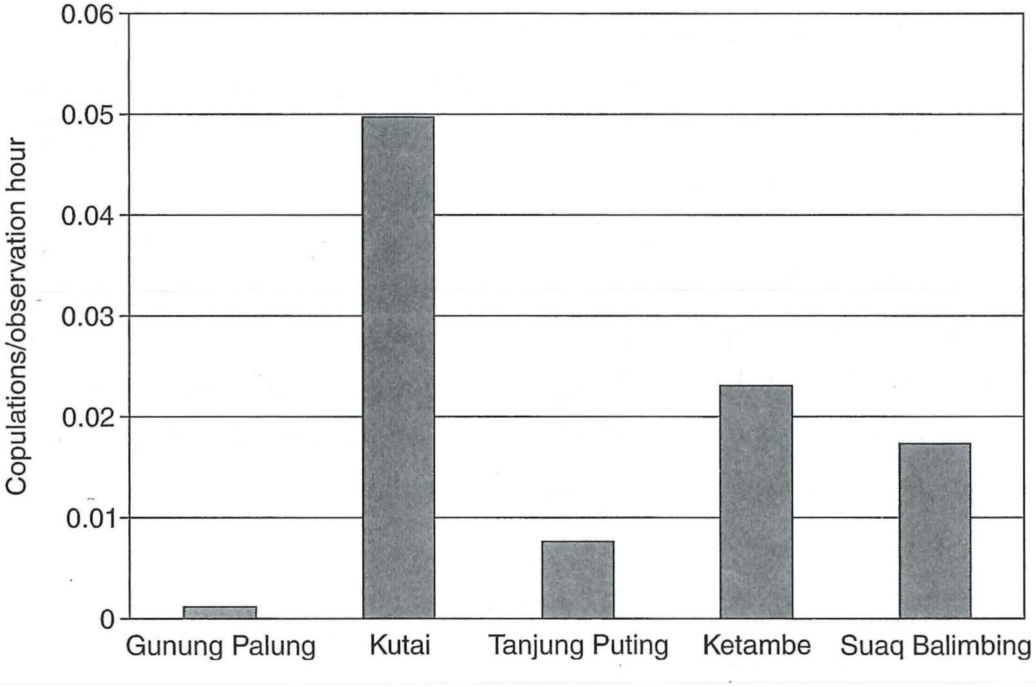

Figure 4.5 Number of copulations observed per hour of observation at five study sites. Samples sizes: Gunung Palung (N=43): Knott et al., in prep; Kutai (N=179): Mitani 1985a; Tanjung Puting (N=52): Galdikas 1985a, b; Ketambe (N=252): Schürmann and van Hooff 1986, Utami Atmoko 2000; Suaq Balimbing (N=156): Fox, 2002.

despite intensive search effort and focal observation time. Thus, at some sites orangutan matings are highly clustered. In contrast, Wich et al. (2006) suggest that at Ketambe (Sumatra) diet composition, copulations, and conception rates show little temporal variation.

Furthermore, the overall ecological productivity of a site is predicted to determine the total density of orangutans, and the number of fecund females may influence the relative proportion of flanged vs. unflanged males, which may in turn influence the total number of copulatory attempts and how these break down between forced and consensual categories. Thus, relative food availability may have an important effect on sexual coercion in orangutans, and analyses of mating behavior should control for food availability. Indeed, at Suaq in Sumatra, Fox (2002) observed almost double the rate of forced copulations by unflanged males during periods of high fruit abundance, although this difference was not significant. These forced copulations were due to an increase in the time these females spent in parties with multiple unflanged males (Fox 2002). Females were more likely to consort with flanged males during months of high fruit availability, or within a week before or after a high fruit abundance month (Fox 2002). Based on inference from evidence at Gunung Palung (Knott 1999), Fox (2002) predicts that these were periods of high conception risk, although this was not explicitly measured. Thus, as food availability changes, female reproductive status may follow suit, changing the dynamics of social encounters and thus the rates of forced versus consensual copulations.

Sampling

Finally, sampling biases inherent in orangutan research should also be considered in evaluating apparent study site differences in forced copulations. Orangutans commonly travel alone or in mother–offspring units, and thus, individual animals must be targeted for focal follows. Mitani (1985a) was specifically targeting males in his study, and this strategy may have partially led to the high rate of copulations he witnessed. In support of this finding, at my study at Gunung Palung, where the apparent copulation rate is low, 74% of focal follows have been on females. Furthermore, differences in the way that forced and consensual copulations are categorized may be important. I would recommend that future studies quantify the components of male and female behavior during mating as described in Knott et al. (in review) in order to use comparable measures between study sites.

Summary of Variables

The above factors, in combination, help explain a large part of the variation in the degree of resistance and proceptivity shown by female orangutans, as well as the level of male aggression. Matings of ovulating females with resident, prime, flanged males during periods of high food availability involve high levels of female proceptive behavior and often no resistance and no aggression. Females may resist these males, however, if they mate with them during the non-POP period. In contrast, POP matings between unflanged or past-prime males that are low-ranking and nonresident involve no proceptive behavior by the female and are often severely resisted. Females may mate cooperatively with these males, possibly as a paternity confusion strategy, particularly during the non-POP period. Females during the first trimester of pregnancy show extreme proceptivity to males and usually mate cooperatively, again as a possible paternity confusion strategy. As the ratio of males to females increases, likely owing to the availability of fecund females, higher rates of forced copulations are seen by both flanged and unflanged males. These complex mating decisions in orangutans can be further illuminated by increased study of endocrine physiology and mating data across sites, controlling for the male:female ratio and food availability at the time of mating.

Male Harassment

Male harassment, the second form of sexual coercion described by Clutton-Brock and Parker (1995), occurs in orangutans within the context of unwanted mating attempts, and sometimes forced consortships, by nonpreferred males. Fox (2002) provides considerable evidence that females seek spatial association with flanged males as a way to distance themselves from unflanged males as a mode of protection. Orangutan females who maintained a spatial association with flanged males received lower rates of harassment (Fox 2002). Fox's (2002) data show that unflanged males were successful during 71% of copulation attempts during days when the female was consorting with the resident flanged male compared to a 95% successful copulation rate for unflanged males when she was not accompanied by the resident flanged male.

Consortships between females and flanged males occur under two contexts: mating and nonmating. During mating consortships Fox (2002) found that unflanged males attempted more matings and had more attempts that were successful compared to nonmating consortships. This was presumably because these consortships occurred when females had a higher probability of conception, and thus the unflanged males made increased efforts to mate. Indeed, Fox (2002) found that parties of unflanged males of three or more always occurred in the context of these flanged male-adult female consortships. Failed mating attempts by unflanged males were due to the female fleeing to within 10 m of the resident flanged male (56%), or the resident male chasing the unflanged male (44%). Interestingly, when females were consorting with nonresident flanged males, the unflanged males spent significantly more time within 50 m of the consorting pair compared to consortships with the resident flanged male. The success rate of copulations with unflanged males was similar, at 60% (Fox 2002). These data indicate that both resident and nonresident flanged males offer a degree of protection for females.

Protection-seeking behavior is seen in other female animals as well. Female African elephants are known to consort with large, dominant males during estrous periods to avoid harassment from subordinate males (Moss 1983). It seems that some female orangutans behave similarly by consorting with flanged males to receive protection from unflanged males.

The second type of consortship between flanged males and females does not involve mating, and Fox (2002) speculates that females initiate these associations purely to reduce harassment by unflanged males. In Fox's (2002) study, these associations often occurred after an unflanged male had forcibly copulated with a female. These nonmating associations differed from mating consortships with flanged males in several important ways. They formed and disbanded after the arrival and departure of the unflanged male, and the flanged male did not chase away the unflanged male. Females clearly initiated these consortships with flanged males, whereas the initiator of mating consortships between females and flanged males was hard to determine. Unfortunately, we do not know the ovulatory status of these consortships, although Fox (2002) speculates that this female was not ovulating.

Intimidation, Indirect Coercion, and Noncoercive Male Aggression

There is no evidence of male aggression toward females outside of the mating context in orangutans. Adult male and female orangutans have very low rates of interaction. When they do interact, it is almost entirely within a mating or consortship context. There is no evidence that males use aggression as a way to control females or to influence future mating behavior of females. They also do not show other forms of noncoercive aggression. Wild male orangutans have never been seen, for example, to "police" female-female aggressive interactions (which themselves are very rare), something that is commonly seen in chimpanzees (Boehm 1994; Kahlenberg unpublished data). Intriguingly, however, this has been reported in captive orangutans (Zucker 1987).

The Cost of Sexual Coercion

Smuts and Smuts's definition of sexual coercion includes the requirement that such aggression occurs as *"at some cost to the female"* (1993:3; my emphasis). Although females frequently try to escape from forced copulations, these attempts are rarely successful (Galdikas 1985a, b; Fox 1998; Fox 2002), which begs the question—why resist? Thus, we can ask what cost do female orangutans suffer as a result of sexual coercion? Possible costs to investigate include (1) physical injury, (2) energetic costs, (3) disease risk, and (4) insemination by a nonpreferred male.

Physical Injury

In many mammals, male sexual aggression against females results in the physical wounding of females. Male hyenas sometimes inflict serious wounds on females during "baiting behavior," which occurs when females are sexually proceptive and is the only circumstance in which males are aggressive toward females (Szykman et al. 2003). Bottlenose dolphin males are responsible for the majority of attacks on adult females that result in tooth rakes and scarring. Moreover, female bottlenose dolphins are most likely to be attacked when cycling as opposed to other reproductive states (Scott et al. 2005). In sea lions, sexual aggression during breeding can result in female injury or even death (Chilvers et al. 2005). In primates, male chimpanzees commonly inflict wounds on females (Goodall 1986; Kahlenberg 2006). Such aggression can be measured in the elevated cortisol levels seen in individual female chimpanzees who were the most common victims of male aggression (Muller et al. 2007).

Therefore, it is surprising that a close reading of published data and descriptions of sexual coercion in orangutans include no indication of wounding of the female by the male. Although forced copulations may include physically aggressive behaviors from males, such as hitting and biting (Galdikas 1981; Mitani 1985), no investigators report that these bites actually broke the skin, that visible wounds resulted, or that females appeared injured after these encounters. This suggests that these bites may actually be "threat" bites not intended to actually inflict harm.

It is certainly possible that occasional injuries could be missed. However, it is unlikely that any serious wounds would not be seen in habituated animals that are followed after the copulation occurs. Flanged males regularly experience wounds from fights with other flanged males (Utami Atmoko 2000; Galdikas 1985b); thus the intentional biting of a restrained victim would certainly result in serious wounding. Males have been seen to die eventually from these wounds (Knott 1998b). In my study at Gunung Palung (Knott 1996), chemstrip analysis of urine showed that wounded males had significantly higher leukocyte levels, compared to females who showed no wounding and no leukocyte excretion in their urine.

Besides open wounds, females could be receiving soft tissue injuries. Such bruises would be very hard to see in the wild and have not been reported. Other obvious injuries from wounding such as limping and favoring a limb have also not been reported. In contrast, such injuries are regularly reported for flanged males as a result of male-male competition. Thus, although the force used by males may hurt females, males seem to rarely, if ever, inflict lasting injuries that compromise health or mobility. The observed level of force may be enough to force females to copulate, and wounding females may be both unnecessary and deleterious to the female's health, and thus not in the male's interest if she were to conceive. It has seemed puzzling that females, particularly nonovulating females, resist male aggression given that they apparently expose themselves to injury. However, these data suggest that females suffer little physical cost from resisting male copulatory attempts.

Energetic Costs

Orangutan females may face a cost in lost feeding time during matings. The entire mating "episode" may consist of a prolonged pre-mating period of resistance, foreplay, or the female waiting as the male slowly approaches, followed by 2 to 36 minutes of actual copulatory thrusting. Is this a significant energetic cost? At Gunung Palung matings occurred during periods of high food availability when, it could be argued, females could more readily afford to lose a few of these excess calories. However, these periods are also very important for storing excess calories as fat, and although lost feeding time during the high fruit period would not compromise a female's daily caloric requirements, it would certainly lessen the number of excess calories she could store against future caloric deficit.

Females may suffer caloric costs during consortships as well. During consortship, males usually follow the female and may even feed in adjacent trees, presumably to avoid foraging conflict. However, Fox (1998) tested the energetic hypothesis and did not find decreased foraging efficiency on days when females had forced consortships. She points to two factors that may have obscured a possible relationship: (1) she did not measure caloric intake and (2) the gregariousness of females at this site meant that she had to control for group size effects. Van Schaik (2004), working at the same site, argues that unwanted consortships may still be energetically costly. In addition, the cost of fleeing from an undesirable male and seeking out and traveling toward a desirable male should also be factored in. These energetic deficits would be compounded with multiple matings and could potentially represent a significant cost. The cumulative cost of multiple matings may be one of the reasons an increase in the number of males compared to females leads to increased female resistance. Clearly, more studies quantifying the energetic costs associated with resistance vs. nonresistance are needed to assess this hypothesis.

Disease Risk

Increased disease risk, from both micro and macroparasites, including sexually transmitted diseases and viruses, may represent a significant cost of copulation in orangutans. Individuals in most orangutan populations are largely solitary or semisolitary, and thus would be expected to have a low parasite load. Nunn et al. (2000) report that species that have a greater copulatory frequency have significantly greater white blood cell counts, which seem to be driven by increased risk of acquiring sexually transmitted diseases. Furthermore, ectoparasites and infectious diseases increase in species with more sociality (Altizer et al. 2003). Thus, consider the orangutan female who primarily interacts with her offspring or closely related female kin. Every six to eight years she becomes fecund and goes through a several month period of dramatically increased contact with new individuals, that is, males with whom she mates. This would be a period of significantly increased disease risk for a female orangutan. Diseases of all types are more readily passed on with increased and repeated contact with the same individual, and with multiple individual contacts.

If disease avoidance is an important factor in the cost of mating for orangutans, I would predict that females would (1) try to limit the number of partners with whom they copulate, (2) resist repeated matings with the same male, (3) particularly avoid mating with transitory males who may bring in new pathogens, and (4) limit the length of the matings. These predictions are all consistent with the observed orangutan mating data. With an increased number of males at a site, females increase their level of resistance. Females often resist mating with a male with whom they have just mated earlier, even a preferred male. Females show clear preference for resident vs. nonresident flanged males. Finally, although Mitani (1985a) found that the overall mating "episode" (including noncontact periods) was longer for resisted matings (Mitani 1985a), Knott et al. (in review) found that the length of copulatory thrusting was significantly shorter in resisted vs. unresisted matings. Thus, female resistance, *regardless of whether it is successful,* may serve the important function of reducing the risk of disease exposure for the female.

Are orangutans more vulnerable to disease risk than are other species? The higher white blood cell count in *Pan* compared to *Pongo* (Nunn et al. 2000) suggests an increased disease exposure in *Pan.* Indeed, at the site with the highest density of males, Ngogo, estrous female chimpanzees mated on average 42 times/day for a 12-hour day (Watts in press) compared to a rate of 1.44 matings/day of association for unflanged males and 1.72 matings/day for flanged males (Mitani 1985a). Thus, the chimpanzee mating system may have led to the evolution of an immune system capable of mounting a significant response to disease exposure, particularly from sexually transmitted diseases (STDs), whereas the normally low rates of interaction in orangutans may have led to an immune system less able to combat the increased disease risk of multiple matings. Thus, when possible, orangutan females should try and resist "unnecessary" mating attempts.

Insemination by a Nonpreferred Male

In orangutans, female resistance to mating attempts seems to be a clear indicator of female choice (Fox 2002). In Knott et al. (in review) we show that male aggression during mating is highly correlated with female resistance. Thus, females show their preference for particular males through their level of resistance and through their proceptive behavior. Males, if nonpreferred, try to overcome this choice through the use of force when necessary. As reviewed earlier, females use a number of criteria for distinguishing between males. All orangutan studies indicate that females normally prefer to mate with prime, flanged males. The endocrinological data at Gunung Palung combined with a continuous measure of proceptivity and resistance show that this preference is most extreme during the POP, indicating a clear preference for these males as fathers of their offspring (Table 4.1). Although specific data on who initiates these flanged male-POP female consortships is lacking, these data clearly suggest that female choice is an important factor. Females may thus be using concealed ovulation as a way of exercising their choice of male partner.

Do males "know" that a female is ovulating? The strongest evidence against such knowledge comes from Nadler's (1982) classic study of mating behavior in captive orangutans. In this experiment, a cycling female and prime flanged male were placed in adjacent cages with a barred door between them that could be slid up or down and left at varying heights. In the first set of experiments the door was left open, allowing the male to access the female whenever he chose; he entered the female's cage almost daily, with frequent forced copulations. In the second experiment the door was left just wide enough that only the much smaller female could go between cages. Under this condition the male showed extreme frustration, first reacting violently by shaking the cage and then presenting his erect penis to the female in an apparent attempt to induce her to enter his cage and mate. However, the female only entered the male's cage during midcycle as evidenced by her hormonal levels. Thus, a female orangutan's proceptive behavior is clearly influenced by her ovarian status, and her actions are likely sending a signal to males that she is receptive. Furthermore, the fecundability of each cycle may be variable. Fox (1998) reports

Table 4.1 Relationship between female ovarian status and male type for orangutan matings with matched endocrinological samples at Gunung Palung.

	Unflanged	Prime Flanged	Past-Prime Flanged
Pregnant	nonresisted	nonresisted	no matings
Non-POP	resisted and nonresisted	resisted and nonresisted	resisted and nonresisted
Near-POP	resisted and nonresisted	resisted	no matings
POP	no matings	nonresisted	resisted

from Sumatra that during one POP period a female repeatedly copulated with a flanged male, but during a subsequent apparently POP period she was not proceptive and the male did not attempt to mate with her. This may have been a reflection of lower levels of ovarian hormones, and thus lower fecundability, of the second cycle. Finally, because proceptivity is very pronounced in females during early pregnancy, when their reproductive state is not yet visible, it is not always an honest signal of fecundability.

Males may look for other cues as well. Females at Gunung Palung attracted the most genital inspection when they were pregnant (Knott et al. in review). Pregnant females did not measure high on other measures of attractiveness even though they showed the highest levels of proceptivity. Males tend to avoid mating with females with small offspring, who are presumably not ovulating (Fox 2002; Knott 1997). Recent data from chimpanzees (Emery Thompson 2005) indicate that high-status males initiate more copulations than expected during the days of a female chimpanzee's estrous swelling when she is most likely to conceive. The mechanisms by which such a signal could be conveyed have yet to be determined, although the possibility of olfactory or pheromonal cues have been suggested. Male orangutans (and chimpanzees as well) may sometimes choose to ignore these signals and gamble that mating could lead to conception. Thus, nonpreferred males may attempt to mate with females whenever they can, and preferred males may attempt non-POP mating when there is increased male-male competition. In the Nadler (1982) experiment, the male who was restricted from accessing the female may have mated with her whenever given the opportunity, even during non-POP, because he had no expectation that he would have access to her during her POP. When the female controlled access, the captive male behaved as do wild males, adopting a "sit and wait" strategy in which the female approaches when she is ovulating.

These findings of clear female preference raise the question of why flanged, prime males are most often the preferred fathers and whether there is really a cost to mating with a nonpreferred male. I believe that there are significant reasons to suspect that resident, flanged, prime males may indeed be higher quality sires. As I argue in Knott (in review), the prime male phase is significantly more energetically expensive than the unflanged male stage. In order to attain flanged status males need to be in excellent energetic condition, which may explain, at least in part, the highly variable timing of the initiation of male flange development (Knott in review). Thus, females may choose males who are flanged as an honest indicator of genetic quality, as they were able to attain flanged status and successfully warded off other flanged males (van Schaik 2004). Furthermore, mating frequently with dominant flanged males may increase the male's paternity confidence and thus the likelihood that he will protect a female's infant from infanticide (van Schaik 2004). In addition, Fox (2002) has shown that flanged males can provide females with protection from mating harassment by nonpreferred males.

Summary of Costs

The varied responses of female orangutans to male mating attempts make sense if the cost of mating cooperatively is normally higher than the cost of resisting. These mating costs include energetic loss, disease risk, and loss of protection from a dominant male. Thus, even with preferred males, females may resist mating when they are not ovulating. In some cases, they may even resist repeated mating attempts with a preferred male during POP if they have already mated that day. During POP, mating carries the potentially important cost of insemination by a nonpreferred male, and mating attempts by such males are fiercely resisted. However, females do sometimes mate with nonpreferred males. They may do so because the male dominance hierarchy is unstable, as in Utami's (2000) study at Ketambe, or mating may be infrequent and thus the cost of an individual mating may be low, such as at Gunung Palung, or they may occasionally mate cooperatively as a paternity confusion/anti-infanticide strategy. This may be particularly important when females become pregnant—a likely explanation for the high rate of proceptivity observed in newly pregnant females (Stumpf et al. 2008).

Orangutan Sexual Coercion in Comparative Perspective

The preceding data show that despite having forced copulations, matings in orangutans do not generally involve wounding. Thus, although the term *forced copulation* conjures up the ultimate violence against a female, the actual physical wounding experienced by female orangutans during these copulations is very low. Rather, the degree of force is a direct response to female resistance (Fox 1998; Knott et al. in prep). This observation is in stark contrast to other species that use much more physical force, particularly in indirect coercion, which can be much more physically injurious than direct coercion. Two closely related species in which indirect sexual coercion is very common and often very injurious are chimpanzees and humans.

Comparison to Chimpanzees

Chimpanzee sexual coercion is dramatically different from orangutan sexual coercion in two major ways: the context of the coercion and the level of violence involved. Chimpanzees very rarely have forced copulations. Instead, coercion is normally in the context of aggression toward estrous females in nonmating contexts. This type of sexual coercion is best described as indirect, compared to the direct coercion seen in orangutans. Chimpanzee coercion involves control of female sexuality and an attempt to influence future female behavior. There is no evidence of this behavior in orangutans. Furthermore, wounding as a result of chimpanzee sexual coercion regularly occurs at some sites (Goodall 1986; Kahlenberg 2006). By contrast, such injuries have never been reported in wild orangutans.

Comparison to Humans

Given the features of orangutan sexual coercion we have outlined, the analogy between this and many forms of human rape warrants discussion. Emery Thompson (Chapter 14 in this volume) makes the useful distinction between stranger and acquaintance rape in humans. In humans, stranger rape results in the most serious wounding due to the violent resistance of the victim and the criminal intent to do harm or the pathological mental status of the perpetrator. By contrast, males who rape known victims rarely inflict injuries, and victims report that the use of physical aggression is secondary to verbal coercion (Emery Thompson, Chapter 14).

Because of the low levels of wounding, forced copulation in orangutans is not analogous to human stranger rape. Although the level of aggression used during forced copulations in orangutans may be similar to that seen with known partners in humans, there are considerable differences. Because human males sometimes do use extreme physical aggression during forced copulations, the threat of force is a primary reason that females may acquiesce to unwanted mating efforts by males. Based on analogy with humans, it has been suggested that orangutan females may also acquiesce during matings in order to avoid injury, particularly from the much larger flanged males. However, since wounding of females during forced copulations has not been reported in orangutans, females may not have the same level of fear of injury from males as female humans do. The level of violence utilized by orangutan males may be sufficient to force a copulation without wounding, as it is in many cases of human rape. Thus, one of the major differences is that in humans there can be intentional infliction of injury and severe wounding. Human males can also use these forms of extreme force against females as a means of punishment for real or imagined sexual transgressions, and as a way to control female sexual behavior, both within and outside of a mating context. This type of sexual coercion is not seen in orangutans.

Sexual Coercion and Social Relationships: Why Are Orangutans Different?

What leads to these differences in the context of sexual coercion and the level of aggression involved? The most obvious answer is differences in the social system of these species. The above contrast leads to the hypothesis that frequent contact between a female and male within the context of a multimale mating system, where a female could potentially mate with multiple males, is more likely to lead to indirect and more violent coercion. How well do these predictions fit the data? Chimpanzees and humans are clear examples of species where there is injurious male coercion within the context of a multimale mating or social system. Excessive violence and nonmating aggression in these species are associated mostly with control of female sexuality and behavior beyond achieving copulation. Intriguingly, bonobos are an obvious exception to this generalization.

In contrast, a more dispersed social system, such as in orangutans, leads to direct coercion within the mating context but not the excessive use of force. Paradoxically, more solitary species have increased vulnerability to sexual coercion, as predicted by Smuts and Smuts (1993), because they do not have the protection of other conspecifics. However, I would argue that this coercion is of a different nature than that experienced by females living within multimale communities. In many ways, orangutans are more similar to many nonprimates in the type of sexual coercion observed. Similar accounts of forced copulations have been noted for bighorn sheep, which, interestingly, may also display alternative male morphs (Smuts and Smuts 1993).

Recommendations for Future Studies

The review presented in this chapter suggests that future work on orangutan sexual coercion should (1) use endocrinological data to determine ovulatory status, as this is one of the most critical determinants of female behavior, (2) quantify the components of each mating interaction in order to look at the degree of resistance, aggression, prosexuality, and female attractiveness, (3) quantify the costs of mating and the cost of successful and unsuccessful resistance, and (4) examine more closely the extent of injuries received by female orangutans.

Comparative studies of sexual coercion in animals should be oriented toward further testing the following hypotheses about the context for sexual coercion and the degree of force that is used. *Hypothesis 1:* Indirect sexual coercion leads to more injurious attacks on females than does direct sexual coercion. *Hypothesis 2:* Where the cost of resistance is high and the benefits of escaping mating are low, convenience polyandry results. Where the cost of mating is high, particularly when high male density produces an increased number of matting attempts, female resistance should increase. *Hypothesis 3:* As the degree of force increases such that the potential costs of resisting increase beyond the benefits of escaping, female resistance will decline in the form of convenience polyandry.

Conclusions

Rather than only being a strategy of unflanged males, forced copulations in orangutans should be seen as simply a *male* strategy—one that can be used by either flanged or unflanged males to overcome female resistance. Whether a copulation is forced or consensual depends on the level of resistance exerted by the female, which is in turn dependent on whether or not the male is preferred, the female's ovulatory status, and the costs of mating vs. resisting. The costs of mating in orangutans include energetic costs, disease risk, loss of protection from a dominant male, and the cost of insemination by a nonpreferred male, whereas the risk of injury from resistance appears low.

Concealed ovulation has confounded our ability to understand the context of sexual coercion in orangutans, but recent endocrinological analyses have helped to illuminate male and female strategies. Females prefer to mate with prime, flanged males during their periovulatory period. However, because of the potential costs of mating, females may sometimes choose to resist matings from preferred males as well as nonpreferred males. Females may actually resist mating with a flanged male when the mating attempt occurs outside of her ovulatory period or when multiple matings are sought on the same day. Similarly, whereas females normally resist mating with nonpreferred males, they sometimes do choose to mate cooperatively with these males during periods when they are not ovulating (pregnancy and non-POP periods). Because of this context, it is suggested that this represents an anti-infanticide strategy of confusing male paternity. In addition, an occasional mating with a nonpreferred male during a nonovulatory period may be sufficiently low cost that it is sometimes not avoided.

Orangutan males use aggression to the extent that it is necessary to achieve copulation. However, this level of aggression has not been reported to result in physical injuries to the female—thus the aggression is not "excessive." This finding is surprising given the characterization of orangutan forced copulations as one of the most extreme forms of male coercion in animals. In contrast to chimpanzees and humans, orangutan males do not use coercion to control female sexuality and future sexual behavior. Thus, Estep and Bruce's (1981) concept of *resisted mating* may be a more appropriate term for orangutans—reflecting the notion that the degree of resistance during the mating is primarily a function of female behavior.

Finally, the comparative data between orangutans and chimpanzees is revealing as to the conditions that prompt direct (as in orangutans) vs. indirect (as in chimpanzees) sexual coercion. Indirect coercion is most commonly a strategy of males living in multimale communities as a way to control future female sexual behavior, whereas direct coercion is a strategy of males living in dispersed male communities as a means of achieving an immediate copulation in the event of female resistance, such as is the case with many birds and insects. The level of force in indirect coercion is greater and often involves wounding, whereas in direct coercion it reflects the level of female resistance. Clearly, the nature of orangutan sexual coercion has often been misunderstood and warrants continued reevaluation.

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