18

Orangutans

Understanding Forced Copulations

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1. Why are orangutans largely solitary in their foraging patterns?
2. How do Bornean and Sumatran orangutans differ behaviorally, and what might explain these differences?
3. What are physical and behavioral similarities and differences between flanged and unflanged males?

INTRODUCTION

Orangutans (genus *Pongo*) represent the extreme of many biological parameters. They are the largest primarily arboreal mammal, have the longest interbirth interval, are the most solitary of the diurnal primates, and are the most sexually dimorphic of the great apes. They range over large areas and have diffuse communities. Additionally, adult male orangutans come in two morphologically distinct types, an unusual phenomenon known as *bimaturism*. This intriguing suite of features has proven difficult for researchers to fully understand. The semi-solitary lifestyle of orangutans, combined with their slow life histories and large ranges, means data accumulate slowly. Also, rapid habitat destruction in Southeast Asia has left only a handful of field sites currently in operation (Figure 18.1 and Table 18.1). Despite these difficulties, long-term behavioral studies and recent genetic and hormonal data now allow us to explore some of the most theoretically interesting questions about this endangered great ape. Here, we summarize our current state of knowledge about wild orangutans and discuss advances in our understanding of one distinctive orangutan behavior—forced copulations.

DISTRIBUTION, TAXONOMY, AND MORPHOLOGY

Present Distribution

Though once found throughout Asia, orangutans now occur only on the islands of Sumatra (Indonesia) and Borneo (specifically the Malaysian states of Sarawak and Sabah and the Indonesian provinces of Kalimantan). Both ecological and anthropogenic factors seem responsible for their range collapse (Delgado and van Schaik 2000). Tropical and subtropical zones shifted during the Pleistocene (Jablonski 1998b, Jablonski et al. 2000), and mean annual temperature rose (Harrison 1999, Medway 1977), leading to habitat constriction. Among other evidence of human influence (Delgado and van Schaik 2000), orangutan remains found in caves in northern Borneo show they were preyed upon by humans (Hooijer 1960, Medway 1977).

Orangutans live in true wet rain forests, with reported average annual rainfall between 2,000 mm (Galdikas 1988) and 4,500 mm (Lawrence and Leighton 1996). The primary habitat types they occupy are peat and freshwater swamps and lowland forests. Orangutans have been found living up to an altitude of 1,200 m; however, in Borneo (but not Sumatra) orangutan density declines with increasing elevation (Husson et al. 2009).

Taxonomic Status

Most researchers classify Bornean (*P. pygmaeus*; Color Plate 33) and Sumatran (*P. abelii*) orangutans as separate species based on molecular and morphological analyses that show interisland differentiation that exceeds or is equal to differentiation between the two species of chimpanzee (e.g., Goossens et al. 2009, Groves 2001a, Guy et al. 2003, Ruvolo et al. 1994, Xu and Arnason 1996). A recent genetic meta-analysis estimates a divergence time between the two species of 2.7–5 million years ago (Steiper 2006). Bornean orangutans show further genetic (Warren et al. 2000, 2001; Zhi et al. 1996) and morphological (Groves 1986, Groves et al. 1992, Uchida 1998) variation that corresponds with populations separated geographically by major rivers. Groves (2001a) thus classifies Bornean orangutans into three subspecies: *P. p. pygmaeus* in Sarawak and northwestern Kalimantan, *P. p. wurmbii* in southwestern and

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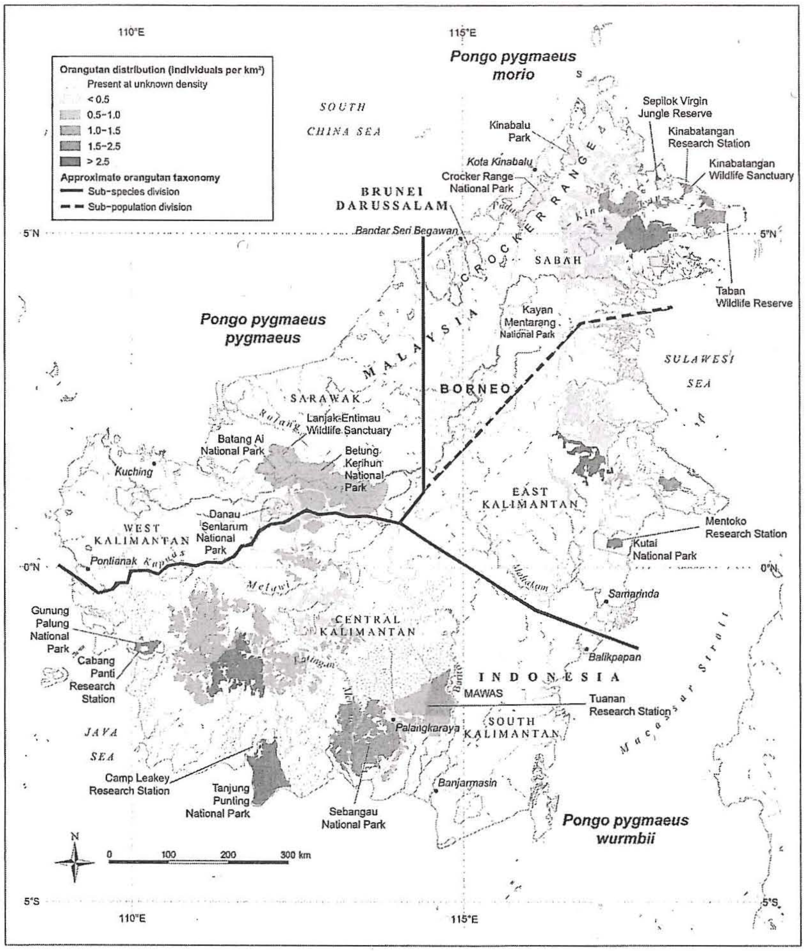

central Kalimantan, and *P. p. morio* in Sarawak and East Kalimantan (Figure 18.1). However, orangutan taxonomy remains controversial. Warren et al. (2001) found genetic evidence for four subpopulations on Borneo that diverged 860,000 years ago, with the *P. p. morio* subspecies being further subdivided into Sabah and East Kalimantan populations. Also, some researchers favor only a subspecies classification between Bornean and Sumatran orangutans (*P. p. pygmaeus* and *P. p. abelii*) (Courtenay et al. 1988, Muir et al. 2000).

Morphology

Often referred to as the "red ape," orangutans have thick reddish-orange hair. They negotiate the canopy through quadrumanual clambering, grasping supports with both their hands and feet (Knott 2004), and by adopting a wide array of body postures (Thorpe and Crompton 2005, 2006). There are no gross differences in positional behavior between orangutan species, but there are differences in the proportion of time spent in various body postures, likely due to habitat differences (Thorpe and Crompton 2005, 2009). Bornean flanged males are reportedly more terrestrial than their counterparts in Sumatra, but this does not hold for all Bornean populations (Knott 2004). Morphological adaptations for arboreality include arms, hands, and feet that are longer than those of humans and the other great apes (Fleagle 1999) as well as a shallow hip joint that allows leg extension of over 90 degrees (MacLatchy 1996). Compared to chimpanzees, orangutans have thicker molar enamel and other dental adaptations associated with their routine ingestion of mechanically hard and tough foods, such as seeds and bark (Vogel et al. 2008).

Orangutans are unusual because males appear to have indeterminate growth, meaning that they gain weight throughout their lives (Leigh and Shea 1995). This growth pattern has been described for only a few other mammals and is thought to be associated with intense male/male competition. Orangutans are also exceptional for having two morphologically distinct types of adult male (Galdikas 1985a,b; Graham and Nadler 1990; Kingsley 1982, 1988; MacKinnon 1979; Maggioncalda et al. 1999, 2000, 2002; Mitani 1985a, b; Schürmann and van Hooff 1986; te Boekhorst et al. 1990). One type is large, weighing over 80 kg in the wild (Markham and Groves 1990), and

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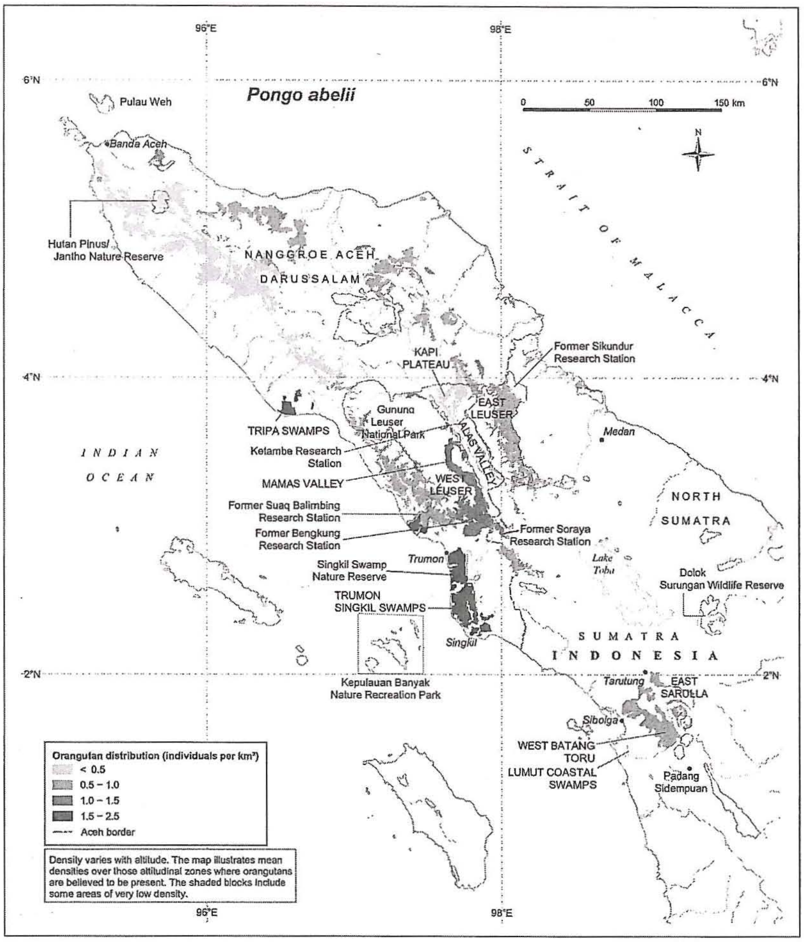


Figure 18.1 Maps of (*A*) Borneo and (*B*) Sumatra, showing species and subspecies distinctions, study sites, densities, and distributions (modified from Caldecott and Miles 2005 and Singleton et al. 2004 by L. Kee and K. Hendrickson).

Table 18.1 Location of Orangutan Field Sites as Referred to in Text

TAXON	FIELD SITE	ISLAND	PROVINCE/COUNTRY
P. pygmaeus morio	Kutai National Park	Borneo	East Kalimantan, Indonesia
	Kinabatangan Wildlife Sanctuary	Borneo	Sabah, Malaysia
P. pygmaeus wurmbii	Gunung Palung National Park	Borneo	West Kalimantan, Indonesia
	Tanjung Puting National Park	Borneo	Central Kalimantan, Indonesia
	Sabangau Ecosystem	Borneo	Central Kalimantan, Indonesia
	Tuanan Field Station	Borneo	Central Kalimantan, Indonesia
P. abelii	Suaq Balimbing Research Station	Sumatra	Gunung Leuser, Aceh, north Sumatra, Indonesia
	Ketambe Research Station	Sumatra	Gunung Leuser, Aceh, north Sumatra, Indonesia

possesses secondary sexual characteristics, including cheek pads called "flanges," a pendulous throat pouch, long hair, and a musky odor (reviewed in Crofoot and Knott in press) (Figure 18.2a). These "flanged" males also produce loud vocalizations, known as "long calls," that are audible to humans up to 800 m away (Mitani 1985b).

The second type of male is half the size of flanged males and does not have secondary sexual characteristics or produce long calls (Figure 18.2b). These "unflanged" males were originally called "subadults" (e.g., Galdikas 1985a,b), but this term is misleading since they are fully capable of siring offspring (Goossens et al. 2009; Kingsley

1982, 1988; Utami et al. 2002). Endocrinological data from unflanged males in zoos show that their gonadotropin and testicular steroid levels are sufficient for spermatogenesis but inadequate for triggering the development of secondary sexual characteristics (Kingsley 1982, Maggioncalda et al. 1999).

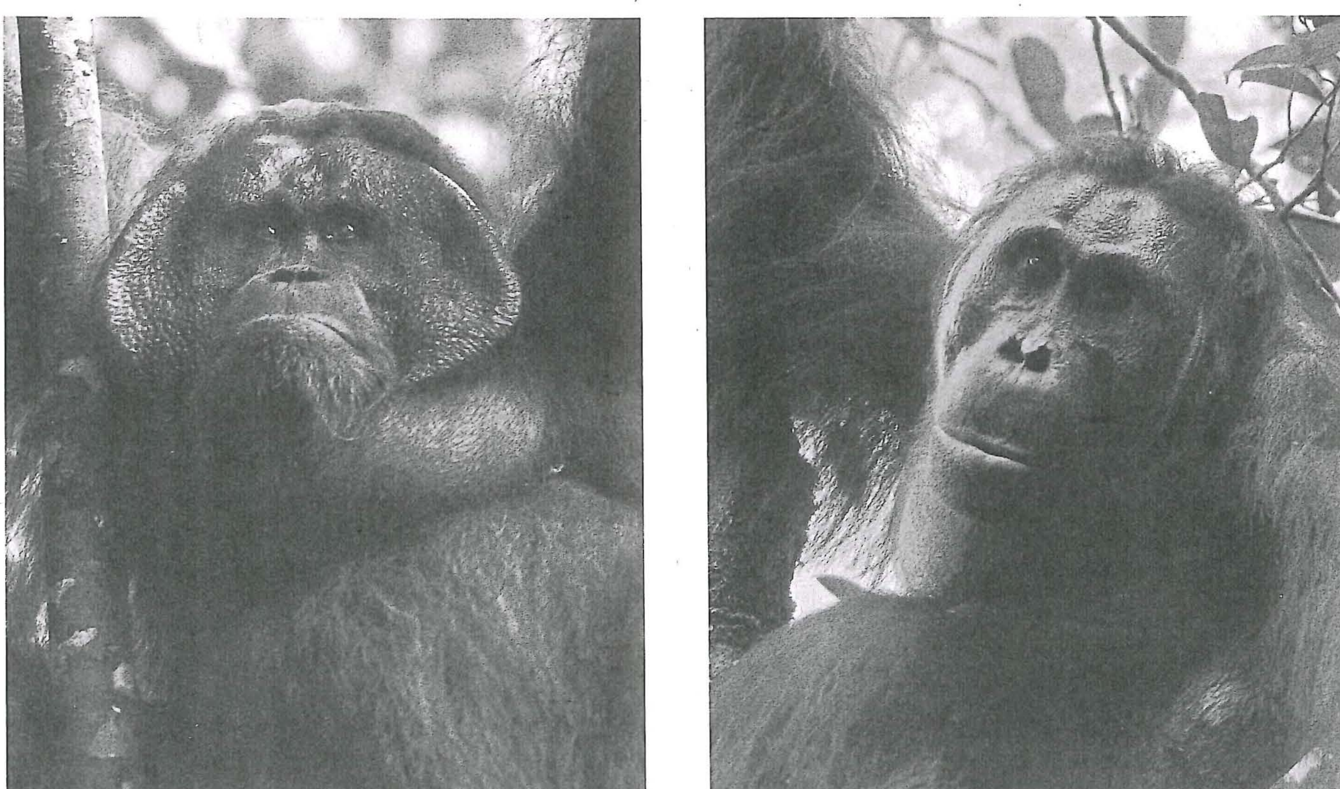
Wild orangutan females weigh on average 39 kg, which is 45% of flanged male body size (Markham and Groves 1990). This makes orangutans one of the most sexually dimorphic species on record. The evolution of extreme sexual dimorphism has been attributed to male/male competition (Rodman and Mitani 1987), female choice (Fox 1998, Utami et al. 2002), and sexual coercion (Smuts and Smuts 1993).

Phenotypic differences between the two orangutan species have been proposed, but no systematic study comparing soft tissue and appearance has been completed. Cranial morphology is highly variable, and more skeletal variation is sometimes found within the Bornean species than between *P. pygmaeus* and *P. abelii* (Courtenay et al. 1988). Among these differences are the shape and profile of the face, the degree of prognathism, the shape of the braincase, and several features of the teeth (Groves 1986, Jacobshagen 1979, Rorhrer-Ertl 1988, van Bemmel 1968). There are differences in jaw structure between the two species, indicating that Bornean orangutans may rely more heavily on hard-to-process foods (Taylor 2006, 2009).

ECOLOGY

Food Availability

The Southeast Asian rain forest is characterized by dramatic fluctuations in the availability of fruit, the preferred food of orangutans. Bornean and Sumatran forests are dominated by trees in the Dipterocarpaceae family that periodically experience a mast fruiting in which up to 88% of the trees of this and other plant families flower and fruit in synchrony (Appanah 1985, Ashton 1988, Cannon et al. 2007, Medway 1972, van Schaik 1986). Mast fruiting occurs every 2–10 years (Ashton 1988), appears to be driven by climatic events associated with the El Niño weather pattern (Curran et al. 1999), and is often followed by periods of extremely low fruit availability (Knott 1998a). Peat swamps are less subject to mast fruiting because of lower dipterocarp density, but fruit availability is still variable (Galdikas 1988). Across study sites, orangutan population density is positively correlated with fruit availability, particularly during periods of fruit scarcity, suggesting that "crunch periods" are important



(A) (B)

Figure 18.2 Photos of (*A*) flanged and (*B*) unflanged males from Gunung Palung National Park (photos by Tim Laman).

for establishing a population's carrying capacity (Marshall et al. 2009a).

Sumatran forests are more productive than Bornean forests since the former have more trees in fruit at any given time, experience more frequent periods of high fruit availability, and have fewer periods of low fruit availability than the latter (Marshall et al. 2009a). Sumatran forests also have higher densities of important orangutan food trees and lower densities of dipterocarp trees than do Bornean forests (Marshall et al. 2009a). This difference in habitat quality likely explains why, in similar habitat types, orangutan densities are higher in Sumatra than in Borneo (Husson et al. 2009). The richer volcanic soil in Sumatran forests seems to underlie inter-island differences in productivity (Delgado and van Schaik 2000).

Diet and Nutrient Consumption

Orangutans feed on twice as many plant genera as do other great apes, and Bornean orangutans feed on more plant species and parts than Sumatran orangutans (Russon et al. 2009b). Sumatran orangutans show less variance in the time spent eating fruit, bark, and leaves and are generally able to maintain a higher level of frugivory in their diet (Morrogh-Bernard et al. 2009). On Borneo, there are periods when orangutan fruit intake reaches 100%, exceeding the highest rates on Sumatra. During low fruit periods on Borneo orangutans eat predominantly leaves and bark (Knott 2005a). Fruit consumption can drop to 10% on Borneo, but it has never been reported to reach below 57% on Sumatra (Morrogh Bernard et al. 2009). Orangutans also incorporate other foods into their diet when fruit is low, such as pithy vegetation and insects, primarily termites (Knott 2005a).

Nutrient intake may vary tremendously. Fruits produced during masts are not only more abundant but also higher in calories, carbohydrates, and lipids (Knott 1999b). When orangutans are subsisting off leaves and bark, fiber comprises a large portion of their diet. Vertebrate animal matter is rarely eaten, but orangutans in Sumatra have been seen opportunistically hunting slow lorises (Utami and van Hooff 1997) and eating a gibbon (Sugardjito and Nurhada 1981). Only one meat-eating observation (a tree rat) has been reported from Borneo (Knott 1998b). Daily caloric consumption has been calculated for Gunung Palung, Borneo, showing dramatic fluctuations associated with fruit availability, with orangutans consuming two to five times more kilocalories during fruit-rich periods compared to fruit-poor periods (Knott 1998a).

Physiologically, orangutans are particularly adapted to fat storage. During periods of high fruit availability, they gain weight, as measured by their intake of significantly more calories than they expend (Knott 1998a). This adaptation appears to have evolved as a way to sustain them through extended periods of low fruit availability when they have been shown, through the production of ketones (Knott 1998a) and the presence of C-peptide in urine (Emery Thompson and Knott 2008), to metabolize their fat reserves. Orangutans on Sumatra may not rely as heavily on fat deposits because they are able to maintain a relatively stable dietary intake (Wich et al. 2006).

Activity Patterns

Orangutans cope with low food availability by being primarily solitary foragers. Across 10 study sites, age/sex class, fruit availability, habitat quality, logging impact, masting versus nonmasting forests, island of origin, and sociality were found to be important predictors of diet and activity patterns (Morrogh-Bernard et al. 2009). Sites where orangutans fed for less than 50% of their active period, on average, were masting, mixed-dipterocarp forests, whereas sites where they fed for greater than 50% of the time were nonmasting, peat swamp forests. Ketambe, in Sumatra, was an exception, a mixed-dipterocarp forest where they fed for greater than 50% of the day. This has been attributed to the site's very high strangler fig density (Wich et al. 2006, Morrogh-Bernard et al. 2009). Orangutans from peat swamp forests generally spent more time feeding and traveling, with Ketambe again being an exception. Orangutans also modify time spent feeding (Galdikas 1988, MacKinnon 1974, Mitani 1989, Rodman 1977), traveling (Galdikas 1988, Knott 1999b, Mitani 1989), and resting (Mitani 1989), as well as their active day length (Morrogh-Bernard et al. 2009), during periods of increased sociality. Across sites, there is a trend for non-sexually active females to feed the most and rest the least, for flanged males to rest the most and feed and travel the least, and for unflanged males to travel the most (Morrogh-Bernard 2009, van Schaik et al. 2009c).

Variability in the food supply seems to explain many of the differences in orangutan foraging strategies and activity patterns (Morrogh-Bernard et al. 2009). At Gunung Palung, a site with highly variable fruit production, orangutans spent more time awake, feeding, traveling, socializing, and mating when fruit availability was high (Knott 1999b). When fruit was low, orangutans conserved energetic resources by spending less time awake and traveling shorter distances per day (Knott 1998c, 1999b). Morrogh-Bernard et al. (2009) call this the "sit and wait strategy" and found it is typical of mixed-dipterocarp forests where mast fruiting results in high variability in fruit production. In peat swamp forests, fruit availability is less variable, leading to a continual "search and find" strategy (Morrogh-Bernard et al. 2009).

LIFE HISTORY

Juvenile Development

Wild orangutans experience very low infant mortality, ranging 7%–17% in Sumatra (van Noordwijk and van Schaik 2005, Wich et al. 2004b); but rates are much higher in captive (Anderson et al. 2008, Cocks 2007) and rehabilitant populations (Kuze et al. 2008). Orangutans spend their first few years in close contact with their mothers, especially during travel when they cling to their mother for the first two years (van Adrichem et al. 2006, van Noordwijk et al. 2009, van Noordwijk and van Schaik 2005). Locomotor competence emerges at around age 3, although some clinging may still be observed up to age 6 and mothers will occasionally use their bodies to bridge tree gaps for older juveniles (van Adrichem et al. 2006, van Noordwijk and van Schaik 2005). Other developmental and social skills gradually develop. Orangutans start building practice nests by age 1 (Prasetyo et al. 2009), but they do not sleep in their own nests until they are 6–8 years old (van Noordwijk and van Schaik 2005). In one study, solitary play was especially prevalent in infants under age 2, and social play began after age 6, peaking at age 8 (van Adrichem et al. 2006).

Infants begin incorporating solid food into their diet at about age 1 or earlier (van Noordwijk and van Schaik 2005). Nursing has been observed up to age 8, although nursing rates appear to be quite low (van Adrichem et al. 2006, van Noordwijk and van Schaik 2005). Juveniles develop feeding independence between ages 3 and 6 (van Adrichem et al. 2006, van Noordwijk and van Schaik 2005). Jaeggi et al. (2008) found that Bornean juvenile orangutans occasionally solicited food from their mothers, with high (>88%) rates of success. Juveniles were more likely to request difficult-to-obtain items, and food-transfer requests decreased with increasing ecological competence (Jaeggi et al. 2008). Overall, immatures seem to be ecologically dependent until ages 8–10, at which time their diet becomes similar to that of their mothers (van Adrichem et al. 2006, van Noordwijk et al. 2009). By age 11, orangutans in Sumatra spend 65% of their time away from their mothers (van Adrichem et al. 2006).

The timing of juvenile development shows important individual and population-level differences (van Adrichem et al. 2006, van Noordwijk and van Schaik 2005). Orangutans in two Bornean peat swamp populations appear to wean their infants earlier than do populations in comparable habitat types in Ketambe (van Noordwijk et al. 2009). However, the general pattern that emerges is one of infant dependence on the mother from 0 to 3 years, a juvenile period between 4 and 8 years marked by increasing competence in foraging and locomotory skills, followed by increasing independence at 8–10 years. Interestingly, orangutans show characteristic changes in the color and distribution of their head and facial hair as well as changes in skin coloration that correspond with these behavioral stages (Kuze et al. 2005).

Male Development

For males, the onset of sexual maturity occurs around age 14 in the wild (Wich et al. 2004b), although the timing of full development of secondary sexual characteristics is highly variable. Some develop into flanged males immediately following adolescence, while others experience maturational delay that can last for a few or many years. At the extreme, wild adult males have been known to remain unflanged for more than 20 years (Utami Atmoko and van Hooff 2004). The variable timing of male development contrasts sharply with the more predictable development of the other great ape males. Maturational delay may be a temporary state, but the possibility that some males never become flanged cannot be rejected (Crofoot and Knott in press).

Unflanged males can develop secondary sexual characteristics in less than a year (Kingsley 1988, Utami and Mitra Setia 1995), caused by a surge in testicular steroids and growth hormones (Maggioncalda et al. 1999, 2000). However, the underlying mechanism that triggers or, alternatively, suppresses development of unflanged males remains elusive. It may be that the presence of flanged males inhibits unflanged male development (Graham and Nadler 1990; Kingsley 1982, 1988; Maggioncalda et al. 1999; Utami Atmoko 2000). However, unflanged males in captivity have fully matured while a flanged male was present (Kingsley 1982, Maggioncalda et al. 1999). Maggioncalda and colleagues (2002) rejected the possibility that "arrested development" in unflanged males is due to chronic stress imposed upon them by flanged males since cortisol, a hormone associated with metabolic and psychosocial stress, is lower in captive unflanged than flanged males. They suggest selection has maintained arrested development as an alternative male reproductive strategy (Maggioncalda et al. 1999). Under this model, males that "play it safe," by postponing the development of secondary sexual features at puberty, avoid the high costs associated with being a flanged male (e.g., male/male aggression, immunosuppression caused by high androgen levels) but are less reproductively successful due to female mate choice for flanged males and reduced competitive ability (Maggioncalda et al. 1999). However, males that experience developmental arrest may achieve approximately the same lifetime fitness as males that "take a chance" (i.e., immediately undergo secondary maturation at puberty) because they end up living longer (Maggioncalda et al. 1999).

Female Development and Ovarian Function

Wild female orangutans reach sexual maturity at approximately 10–11 years (Knott 2001). Like most other primates, they experience a period of adolescent subfecundity, which lasts 1–5 years (Knott 2001). Age at first birth has been reported as between 12 and 16 years in the wild. (Knott 2001, Wich et al. 2004b). As in humans, the menstrual cycle averages 28 days (Knott 2005b, Markham 1990, Nadler 1988). Gestation in orangutans is approximately 8 months (Markham 1990). Pregnancy is recognizable to human observers by a slight but conspicuous swelling and lightening in color of the perineal tissues (Fox 1998, Galdikas 1981b, Schürmann 1981). Orangutans exhibit no sexual swellings or other outward indicators of ovulation (Graham-Jones and Hill 1962, Schultz 1938a). Thus, ovulation appears to be effectively concealed from males (Nadler 1982, 1988; Fox 1998).

Orangutans give birth only once every 7–9 years, on average (Galdikas and Wood 1990, Knott 2001, van Noordwijk and van Schaik 2005, Wich et al. 2004b). Why should orangutans give birth so rarely? Due to the low fruit availability in Southeast Asian rain forests, orangutans may spend significant periods in negative energy balance, when their ovarian function is suppressed (Knott 1999b; Knott et al. 2009). This, in combination with postpartum amenorrhea, may lengthen the time between conceptions (Knott 1999a,b). Additionally, many tree species have long intervals between fruiting, and juveniles may need extended periods to learn the location and processing techniques of difficult foods (van Adrichem et al. 2006, van Noordwijk and van Schaik 2005). Extended time may also be needed to develop social skills before becoming largely solitary (van Noordwijk and van Schaik 2005). Orangutan females in Sumatra have longer interbirth intervals than their Bornean counterparts (Wich et al. 2004b), which is surprising given the greater habitat productivity of Sumatra and, thus, expected higher energetic status of Sumatran females (Knott et al. 2009). Wich et al. (2004b) suggested that this difference may reflect selection for a slower life history in Sumatran orangutans; however, there are no other life history differences between the two species in either the wild or captivity (Anderson et al. 2008, Cocks 2007, Knott et al. 2009, Wich et al. 2009) as would be expected if this was a species difference. Current studies are investigating this paradox.

SOCIAL ORGANIZATION

Grouping Patterns and Philopatry

Although orangutans are predominantly solitary, three types of groupings can be distinguished (Utami et al. 1997): *travel bands* (individuals co-feed and travel together during periods of high food availability), *temporary feeding aggregations* (individuals feed together during times of food scarcity but travel independently), and *consortships* (a receptive female travels in a coordinated fashion with a flanged or unflanged male for several hours, days, or weeks). Additionally, a mother and her dependent offspring may travel with an older daughter and her offspring. At some sites, such as Suaq, orangutans have been observed to be particularly gregarious (van Schaik 1999).

Feeding competition is intense in orangutans and likely explains their largely solitary lifestyle. Orangutans feed in trees that are significantly smaller than those utilized by chimpanzees and bonobos (Knott 1999a,b) and experience periods of much sparser food availability. Orangutan feeding competition mainly takes the form of *scramble competition*, where individuals compete indirectly for patchily distributed food sources. Contest competition also occurs in large fig trees (Sugardjito et al. 1987, Utami et al. 1997). Predation probably plays an insignificant role in regulating grouping patterns; the only reports are of clouded leopards on Sumatra killing ex-captive juveniles traveling without a mother's protection (Rijksen 1978).

In contrast to the other great apes, orangutans appear to be female-philopatric (Galdikas 1988, Knott et al. 2008, Rijksen 1978, Rodman 1973, Singleton and van Schaik 2002, van Schaik and van Hooff 1996). Yet, genetic data show similar relatedness in both sexes (Goossens et al. 2006b, Utami et al. 2002). However, complicating factors exist at both of the sites where genetic data have been reported so far. At Ketambe, individuals were largely unrelated (Utami et al. 2002), but for females this is likely due to the introduction of two rehabilitant females in the late 1970s (Mitra Setia et al. 2009). In Kinabatangan, individuals showed high levels of relatedness, but anthropogenic factors may have affected dispersal options (Goossens et al. 2006b). Dispersal patterns should become clearer as genetic data accumulate.

Social Relationships

Orangutan social interactions are more limited than in many other primates, with some individuals spending days or weeks without contact with conspecifics. Mean party size ranges 1.5–2.0 in Sumatra and 1.05–1.3 in Borneo (van Schaik 1999). Mothers with unweaned offspring are less gregarious than females with older or no offspring (Mitra Setia et al. 2009, van Noordwijk et al. 2009). Orangutans also rarely groom themselves or others. Despite their semi-solitary nature, behavioral and experimental evidence suggests that individualized relationships exist (Delgado and van Schaik 2000, van Schaik and van Hooff 1996, Mitra Setia et al. 2009).

Female Ranging and Relationships

Adult female home ranges overlap considerably (Galdikas 1988; Singleton and van Schaik 2002; van Schaik and van Hooff 1996), for example, 67.8% at Gunung Palung (Knott et al. 2008); and clusters of related females may interact frequently (Knott et al. 2008, Singleton et al. 2009, Singleton and van Schaik 2001). Female ranges vary from less than 200 ha to greater than 850 ha and are smallest in eastern Borneo, where more bark and leaves are consumed, compared to Sumatra, where orangutans are more frugivorous (Singleton et al. 2009). Populations living in more heterogeneous habitats also have larger home ranges (Singleton et al. 2009). Females' day ranges vary from 150 to 1,000 m (Singleton et al. 2009).

Knott et al. (2008) report that despite significant home range overlap, some females at Gunung Palung rarely encounter each other because females maintain distinct core areas with minimal overlap (13.4%) within their ranges. Most females encountered other females less than expected by chance, except for mothers and daughters, which had higher than expected encounter rates. One dyad with encounters at the predicted level also had the highest level of agonism. Though aggression is rare, resident females were more likely to win fights within their own core areas (Knott et al. 2008). Mothers may also intercede in altercations between their daughters and other females (Knott et al. 2008, Singleton et al. 2009). Evidence of female dominance relationships exists (Utami et al. 1997, Knott et al. 2008). It is possible that orangutan females use passive range exclusion to reduce the effect of scramble competition and lower the frequency of contest competition (Knott et al. 2008).

Male Ranging and Relationships

Male orangutans were once thought to defend exclusive home ranges (Rodman 1973), but it is now known that flanged male ranges overlap considerably (Knott 1998c, Singleton and van Schaik 2001). Much less is known about male range size because males travel outside the boundaries of orangutan study sites. Singleton and van Schaik (2001) estimated that ranges for flanged and unflanged males are at least 2,500 ha. Flanged male ranges are three to five times the size of female ranges (Utami Atmoko et al. 2009a) and, thus, overlap the ranges of multiple females (Galdikas 1979, 1985a; Mitani 1985a; Utami and Mitra Setia 1995). Some flanged males remain in a fixed area (residents), while others range over greater regions (nonresidents). However, nonresidents may not be true transients but just rarely encountered males with very large ranges (Mitra Setia et al. 2009). The home range of the dominant flanged male may be smaller than those of other flanged males, which enables the dominant male to closely monitor females within his range (Mitra Setia et al. 2009, Utami Atmoko et al. 2009a). Patterns of male residency are not permanent, however, as males are known to leave an area voluntarily (Galdikas 1979) or can be forced out by nonresident or resident challengers (Utami and Mitra Setia 1995).

Male long calls appear to act as an important mechanism by which relationships are communicated within the dispersed society (Delgado and van Schaik 2000). One flanged male can sometimes be recognized as dominant over all other males (Mitra Setia et al. 2009), although the length of the dominant male's tenure varies. When there is a dominant flanged male, he gives long calls at the highest rate (Delgado 2006, Galdikas 1983, Mitani 1985b, Mitra Setia and van Schaik 2007, Utami and Mitra Setia 1995). Individual long calls show clear acoustic differences (Delgado 2007) that can be identified at least until 300 m (Lameira and Wich 2008). Flanged males are totally intolerant of other flanged males and subordinates may monitor the dominant male's long calls to avoid altercations (Mitani 1985b). Dominant males are most likely to approach the long calls of subordinate flanged males (Mitra Setia and van Schaik 2007). Males are less likely to call when in the presence of a female (Mitani 1985a), presumably to avoid attracting the attention of more dominant males (Mitra Setia and van Schaik 2007). Recent data from Sumatra confirm that the primary function of long calls is to attract females (Mitra Setia and van Schaik 2007), as has been proposed by earlier researchers (Delgado 2006, Fox 2002, Galdikas 1983, Utami Atmoko 2000, Utami and Mitra Setia 1995).

Flanged males are invariably dominant to unflanged males, as evidenced by observations of unflanged males fleeing from flanged males (Galdikas 1979, 1985a,b; Mitani 1985a; Utami Atmoko 2000) and being supplanted in fruit trees (Utami et al. 1997). However, flanged males are markedly more tolerant of unflanged than flanged males and often allow them to remain in proximity undisturbed (Galdikas 1985a). This tolerance is not due to the males being closely related (Utami et al. 2002), and it wanes when a potentially reproductive female is present (Galdikas 1985a,b; Utami Atmoko 2000). Unflanged males may try to remain near a flanged male when he is consorting with a female, and aggressive encounters between these males occur in this context more often than when females are absent (Utami Atmoko et al. 2009a). Unflanged males often travel together (Utami Atmoko et al. 2009b), usually without aggression (Galdikas 1985b, Mitani 1985a), although aggression is more common in the presence of females (Utami Atmoko et al. 2009a). Dominance relationships among unflanged males have not been fully described, but observations of approach–avoidance interactions, aggression, and mating interruptions involving these males suggest that dominance relationships exist (Galdikas 1979, 1985b; Utami Atmoko 2000). The ratio of flanged to unflanged males varies between populations (Utami Atmoko et al. 2009b) and is highly variable within a population, probably related to food availability and the presence of receptive females. Formerly dominant flanged males are called "past prime" because they show greatly diminished cheek flanges, give fewer long calls, have lower testosterone levels, mate infrequently, and are subordinate to "prime" flanged males (Knott 2009).

Male–Female Relationships

It has long been assumed that there were no long-term relationships between male and female orangutans, but recent reports suggest that, at least in Sumatra, females may maintain loose associations with the dominant flanged male in the area. Females seek out this male for protection from male harassment and possibly from infanticide. At Suaq, females that associated with a flanged male received less harassment from unflanged males seeking copulations (Fox 2002). Additionally, some of these associations did not involve mating with the dominant male but were female-initiated and disbanded after the unflanged male left the area (Fox 2002). Mitra Setia and van Schaik (2007) argue that males play a protective role since Ketambe females of all reproductive states responded to male long calls by traveling toward those males. Additionally, although rare, food transfer sometimes occurs between adult orangutans, particularly between sexually active females and unflanged males (van Noordwijk and van Schaik 2009).

Mating Behavior

Orangutan copulations normally occur face-to-face, are extremely long in duration (average 8–11 min), and often involve extensive precopulatory behavior and forced copulations (Fox 1998, Galdikas 1981b, Knott 2009, MacKinnon 1979, Mitani 1985a, Stumpf et al. 2008, Utami and van Hooff 2004). Copulatory frequency is fairly low, occurring at a rate of 0.002–0.14 copulations per observation hour (Stumpf et al. 2008). Young females are often particularly proceptive (Galdikas 1979, 1981b; Schürmann 1982; Schürmann and van Hooff 1986). Females sometimes play an active role during mating by aiding with intromission, manually or orally stimulating male genitalia, and performing pelvic thrusts (Fox 1998; Galdikas 1979, 1981b; Schürmann 1981, 1982; Utami Atmoko 2000).

Sexually receptive females express mating preferences for the resident dominant flanged male (Fox 1998, Utami Atmoko 2000, Knott 2009, Knott et al. 2010). Flanged males predominantly use a "sit-call-and-wait" strategy, whereby they advertise their presence with long calls and wait for females to approach and establish a consortship (Galdikas 1985a, Utami and van Hooff 2004). At Gunung Palung, females encounter prime flanged males at a higher rate around the time of ovulation, and this is likely a female-driven outcome (Knott et al. 2010).

While on consort, flanged males closely guard females and react aggressively to the calls or presence of other males, including unflanged males that often follow consorting pairs (Galdikas 1981b). If two flanged males meet in the presence of a receptive female, escalated contests often ensue, and the dominant male will take over a subordinate male's consortship (Galdikas 1985a). Wounds suffered during male/male fights can be serious (Galdikas 1985a) and even fatal (Knott 1998b). Participating in consortships is costly for flanged males because they must adjust their normal activity budgets to accommodate the longer day ranges of females (Mitani 1989, Utami Atmoko and van Hooff 2004). Flanged males are therefore somewhat selective and sometimes reject or react passively to nulliparous females but readily accept parous females as consort partners (Galdikas 1981b, 1985a, 1995b; Schürmann 1981, 1982). Such selectivity is likely adaptive since young females have a higher probability of being subfecund.

Unflanged males usually adopt a lower-profile mating strategy in which they do not emit long calls or form consortships but instead actively search for mating opportunities (Galdikas 1985a,b). Females are generally not proceptive toward these males when they are ovulating (Knott et al. 2010), but unflanged males try to copulate despite female resistance. Outside ovulation, females may show little resistance and even proceptive behavior toward these males (Knott et al. 2010). Female orangutans show strong mating preferences as evidenced by both forceful resistance and extreme proceptivity. Functional explanations for this behavior are explored in the are explored below in the "Discussion" section.

TOOL USE AND CULTURE

Tool use for extractive foraging is relatively rare in wild orangutans (van Schaik et al. 1999a). The site with the most habitual tool use is Suaq, where orangutans strip sticks and use them to harvest insects and *Neesia* seeds (Fox et al. 1999; van Schaik and Knott 2001; van Schaik et al. 1996a). Tool use for *Neesia* seed extraction seems to be a cultural difference as orangutans at Gunung Palung regularly eat this fruit but do not use tools to access seeds (van Schaik and Knott 2001). Orangutans may invent tool use at a fairly constant rate, but the high density of individuals at Suaq may permit increased transmission and diffusion throughout the population (Fox et al. 2004, van Schaik 2002, Whiten and van Schaik 2007). The strong association of mean female party size with tool-use specialization supports this hypothesis (van Schaik et al. 2003b).

Orangutans show many population-level innovations. These are novel learned behaviors that are not simply a result of social learning or environmental induction (Ramsey et al. 2007, Russon et al. 2009a, van Schaik et al. 2006) and include other types of tool use. van Schaik et al. (2009a) recently identified 54 innovations across eight orangutan sites, with 26 reaching cultural significance. Some cultural innovations involve leaves used in agonistic displays (Galdikas 1982a, MacKinnon 1974, Rijksen 1978), for self-cleaning (MacKinnon 1974, Rijksen 1978), as protection in food acquisition (Rijksen 1978), and as drinking vessels (Knott 1999a). Sticks have been used for scratching (Galdikas 1982a) and dead wood for opening up durian fruits (Rijksen 1978). Other behaviors, such as the use of "leaf umbrellas" during rainstorms, are considered a cultural universal (van Schaik et al. 2003a). Orangutans also show flexibility in their sounds and vocalizations. Thirty-two calls have been identified, many of which may be cultural innovations (Hardus et al. 2009). Intriguingly, ex-captive rehabilitant orangutans generate more innovative behaviors than their wild counterparts (Russon et al. 2007), many involving groundwater, which wild orangutans typically avoid (Russon et al. 2009a). This may be due to a lack of maternal guidance that allows these young individuals to invent their own solutions (Russon et al. 2009a). Differences between wild populations in the size of the cultural repertoire are predicted by the opportunity for oblique and horizontal transmission during development (van Schaik et al. 2003b), which may also be applicable to the rehabilitant case.

CONSERVATION

The IUCN Red List (IUCN Species Survival Commission 2008) classifies Bornean and Sumatran orangutans as endangered and critically endangered, respectively. In 2004, there were approximately 54,000 orangutans remaining on

Borneo and 6,500 on Sumatra (Wich et al. 2008). The minimum viable population size is 250 orangutans (Singleton et al. 2004, Marshall et al. 2009b), and presently only six populations on Sumatra and 32 on Borneo meet this criterion (Wich et al. 2008). Genetic analyses indicate that orangutan populations in Sabah have declined by 95% in the last few centuries, with a massive collapse in the last few decades coincident with anthropogenic forest exploitation (Goossens et al. 2006a). Sharp population declines have also been reported for other parts of Borneo and Sumatra and have been linked to recent human activities (Rijksen and Meijaard 1999, Robertson Yarrow and van Schaik 2001, van Schaik et al. 2001).

The main threat to orangutans is habitat loss and fragmentation. Between 1992 and 2002, 2.8% of orangutan habitat in Kalimantan was destroyed annually (Wich et al. 2008). Between 1985 and 2001, 1%–1.5% of orangutan habitat in Sumatra was lost per year (Singleton et al. 2004). Forests have been cleared for logging, mining, and agriculture. Habitat loss has accelerated recently due to the rapid expansion of oil palm plantations. Palm oil is in high demand globally for its use in cooking, in cosmetics, and as a biofuel. Indonesia and Malaysia produce the vast majority of the world's palm oil. On Borneo, the total area planted with oil palm increased from 2,000 km² in 1984 to 27,000 km² in 2003, and much of this converted area was prime orangutan habitat (Ancrenaz et al. 2008). Orangutan habitat has also been destroyed by fire, linked to droughts caused by El Niño climatic events. As a result of the 1997–1998 fires, the number of Bornean orangutans was reduced by about 33% in a single year (Ancrenaz et al. 2008).

About 75% of orangutans occur outside national parks (Meijaard and Wich 2007) and often in forests that are legally exploited for timber or agriculture. Logging is generally associated with a decline in orangutan density (Felton et al. 2003, Husson et al. 2009, Johnson et al. 2005, Morrogh-Bernard et al. 2003, Rao and van Schaik 1997, van Schaik et al. 2001), likely because it reduces food availability and introduces gaps into the canopy, making travel more difficult (Rao and van Schaik 1997). However, the extent of orangutan population disturbance depends on the intensity of logging, with lightly logged forests supporting more orangutans than heavily logged forests (Ancrenaz et al. 2005, Husson et al. 2009). Bornean orangutans display greater dietary flexibility, which might explain why *P. pygmaeus* populations are less disturbed by logging than *P. abelii* populations (Husson et al. 2009). Orangutan densities can recover to prelogging levels if forests containing adequate orangutan foods are allowed to regenerate (Knop et al. 2004). Habitat loss is a major threat to orangutans even within designated protected areas since most national parks have been seriously degraded as a result of inadequate law enforcement (Jepson et al. 2001, Nellemann et al. 2007, Robertson Yarrow and van Schaik 2001). Between 1985 and 2001, over 56% of Kalimantan's lowland rain forests within protected areas were destroyed (Curran et al. 2004).

Although prohibited by law, hunting is another major factor contributing to orangutan population decline (Marshall et al. 2006, 2009b). Orangutans are killed for food, for use in traditional medicines, as retribution for crop raiding, and to obtain infants for the illegal pet trade (Rijksen and Meijaard 1999). In 2003–2004, 200–500 orangutans from Kalimantan were lost to the pet trade (Nijman 2005). Orangutan mothers are typically killed in the capture process. Logging often exacerbates hunting pressures because it creates easier access to forests via construction of new roads. Even if habitat is not lost, orangutan populations cannot survive an annual removal rate of 1%–2%, due to their very long inter-birth intervals (Marshall et al. 2009b). This rate is likely exceeded in many populations.

Although the situation facing orangutans is dire, progress in orangutan conservation has been made. Forest loss has slowed in some orangutan strongholds (Meijaard and Wich 2007, Wich et al. 2008), and illegal logging within national parks has also dramatically declined in several areas (Wich et al. 2008). These changes can largely be attributed to increased political and financial support and efforts by local and international nongovernmental organizations. Though encouraging, such improvements must be considered fragile as threats to orangutans abound and conservation progress can be quickly reversed.

DISCUSSION: UNDERSTANDING FORCED COPULATIONS

One of the most striking features of orangutan biology is the regular occurrence of forced copulations. Male aggression in the mating context is not unique to orangutans (van Schaik et al. 2004, Muller and Wrangham 2009), but forced copulations are remarkably rare in primates. Although forced copulations have been thought to primarily be a mating strategy of unflanged males (Rijksen 1978; Galdikas 1979, 1981b; Schürmann 1982; Fox 2002), observations across study sites show that both flanged and unflanged males engage in this behavior (Figure 18.3). Orangutan mating involves both resistant and cooperative female behavior (Table 18.2), and the nature of female behavior can switch within a given mating interaction as well as between copulations on the same day (Rijksen 1978; Galdikas 1981b; Mitani 1985a; Fox 2002; Knott 2009). These observations are puzzling. Given that females seem to prefer flanged males, why do they sometimes resist these males and, alternatively, why do they sometimes mate cooperatively with less preferred unflanged males? Recent evidence demonstrates that female orangutans adopt multiple strategies, depending on their own reproductive state, the identity of their mating partner, and other considerations (Stumpf et al. 2008, Knott 2009).

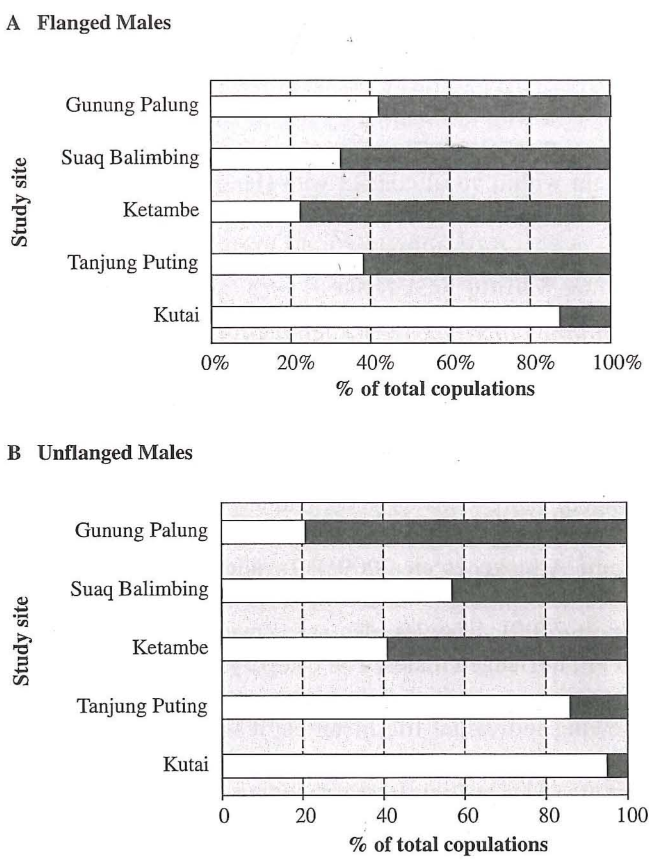


Figure 18.3 Proportion of forced and cooperative matings at major orangutan study sites for (*A*) flanged and (*B*) unflanged males. White bars indicate percentage of matings that were forced (i.e., females resisted), and black bars indicate percentage of matings that were cooperative. Sample sizes are for copulations of known outcome and are as follows (unflanged/flanged): Gunung Palung, *n* = 24/19 (Knott et al. 2009a); Suaq Balimbing, *n* = 90 with known outcomes/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).

Female Proceptivity and Cooperative Mating

The Good Genes Hypothesis

The preference that orangutan females have for flanged males has been interpreted as a female's effort to obtain "good genes" (Galdikas 1981b; Mitani 1985b). Female orangutans give birth to only a few offspring over their lifetime, invest heavily in each one, and have very high infant and juvenile survivorship. Such heavy investment is predicted to lead females to choose males with the best genetic makeup to father their young. Since it has been assumed that dominant flanged males sire the majority of offspring, selection for good genes has been a plausible explanation for why females resist subordinate males and mate cooperatively with the dominant flanged male. Recent genetic data (Goossens et al. 2006b) confirm greater reproductive success for flanged males. Because not all males can become flanged and the flanged stage is energetically costly, this may serve as an honest signal of male quality (Knott et al. 2010).

Table 18.2 Possible Explanations for Orangutan Female Cooperation and Resistance During Mating

FEMALE COOPERATION	FEMALE RESISTANCE
Paternity concentration in dominant male	Paternity avoidance of subordinate or unpreferred/unflanged male
Paternity confusion with potentially infanticidal males	Avoidance of unnecessary contact to limit disease transfer
Avoidance of sexual coercion/harassment if no risk of conception	Elicitation of support from dominant male
	Prevention of feeding/energetic costs
	Prevention of ejaculation
	Mate assessment

Paternity Confusion to Prevent Infanticide

There is substantial evidence, across mammalian taxa, that males sometimes use infanticide as a reproductive strategy (see reviews by Hiraiwa-Hasegawa 1988, Hrdy and Hausfater 1984a, van Schaik 2000b; but see Bartlett et al. 1993, Sussman et al. 1995). By killing infants they have not sired, males can create a new reproductive opportunity by interrupting a mother's lactational amenorrhea, causing her to return to a fecund state sooner than would occur otherwise (Hrdy 1979). Given their slow life histories and high lactation-to-gestation ratio, female orangutans, along with the other great apes, should be among the primates most vulnerable to infanticide (van Schaik 2000b).

One way for females to decrease the risk of infanticide is to use sexual behavior (Hrdy 1979). Because males do not recognize their offspring, females are expected to mate with potentially infanticidal males when possible, including when conception is unlikely, to increase these males' assessments of likely paternity. If a newly dominant male is reasonably uncertain about whether he sired an infant, it benefits him, in terms of fitness, to refrain from killing the infant (van Schaik et al. 2004). Thus, if female orangutans can recognize that a dominant male may be overthrown before the birth of their next infant, the infanticide-avoidance hypothesis predicts that they should willingly copulate with up-and-coming unflanged males or flanged males that are likely to be successful in challenging the dominant male. Observations from Ketambe in Sumatra are consistent with these predictions. When a single dominant male could not be recognized, females, including those that were lactating and pregnant, readily copulated and formed consortships with unflanged and subordinate flanged males (Utami Atmoko 2000). Paternity data also indicate that female orangutans may be able to recognize males rising in rank because one unflanged male at Ketambe, which later became dominant, fathered 50% of offspring sired by unflanged males (Utami et al. 2002).

Recent data from Gunung Palung (Knott et al. 2010, Knott 2009) provide new support for the infanticide-avoidance hypothesis. The lower the likelihood of females getting pregnant, the more proceptive and cooperative they were to unflanged and past-prime flanged males during mating. Females mated most frequently with unflanged males when their conception risk was low, and these copulations were often consensual. At the beginning of pregnancy, before females show the characteristic labial swelling, they were extremely proceptive. Females facilitated penetration and engaged in oral contact with male genitalia, particularly when mating with prime flanged males. Other evidence of perceived infanticide risk comes from play-back experiments, which demonstrate that while females and infants ignore the long calls of resident flanged males, they show strong negative reactions to the vocalizations of nonresident males (Delgado 2003). Further, females with infants move toward flanged male long calls, which Mitra Setia and van Schaik (2007) interpret as an anti-infanticide strategy.

The most serious problem with the infanticide-avoidance hypothesis is that, despite nearly four decades of study, successful or attempted infanticides have never been reported in wild orangutans (Beaudrot et al. 2009), although there is one case of infanticide reported from captivity (Mallinson 1984). The absence of infanticide is surprising since it has been recorded in other great apes (chimpanzees, reviewed by Stumpf this volume; gorillas, Watts 1989b, Robbins this volume), with the exception of bonobos. However, because the average party size is much smaller in orangutans, the number of "ape-hours" observing chimpanzees and gorillas is much higher than in orangutans, and slow reproduction and low interaction rates may present limited opportunities for infanticide to occur and be observed (Stumpf et al. 2008, Knott et al. 2009). In a recent consideration of this hypothesis, Beaudrot et al. (2009) argue that the conditions for infanticide are so rarely met that we should not expect it to occur. However, the mounting evidence that females are engaging in infanticide-avoidance strategies suggests that the high potential cost of an infant loss may result in counterstrategies to infanticide, even when the probability of such an event is low.

Avoidance of Harassment

Females may mate cooperatively as a way to avoid harassment. Such a strategy would lead to the prediction that as male density, and thus potential harassment, increases, females should show less resistance. This behavior is seen in some species and has been termed "convenience polyandry" (Low 2005). However, Knott (2009) found that populations that had a higher male-to-female ratio had more, not less, female resistance to both flanged and unflanged males. Instead of acquiescing, females respond to male harassment by either resisting during mating or increasing their proximity to the flanged male. Fox (2002) shows that females at Suaq received lower harassment if they remained close to or consorted with the dominant flanged male, and Mitra Setia and van Schaik (2007) suggest that females at Ketambe may remain within vocal contact with flanged males to reduce harassment.

Female Mating Resistance

Avoidance of Undesirable Paternity

Given that females prefer flanged males and their potentially superior genes, why do they sometimes resist mating with these males? Females may not prefer just any flanged male. When there is a clearly dominant resident flanged male, females show the highest preference for that male, rejecting other flanged males (Mitani 1985a; Utami Atmoko et al. 2009a). In addition, females may reject some flanged males because they are past-prime (Knott 2009). Females also resist mating with some, but not all, unflanged males. The category of unflanged males encompasses multiple developmental stages. Without knowing individual life histories, it is difficult to distinguish unflanged males that are adolescents from those that are older but have remained in an unflanged state and those that are in the process of becoming flanged (Knott 2009). The distinction may be very important to females in their mate assessment. Fox (1998) found that females behaved very differently toward small, medium, and large unflanged males. Female behavior is consistent with the possibility that they are aware of changing male status before researchers are since they seem to anticipate these changes. At Ketambe, Utami Atmoko (2000) found that an unflanged male with whom females mated cooperatively developed cheek pads and displaced the dominant flanged male six months later. Additionally, females started preferentially approaching the long calls of the new dominant male in the period *before* he became dominant (Mitra Setia and van Schaik 2007).

Disease Avoidance

Orangutan females seem to be surprisingly mating-averse. A female who mates cooperatively with a dominant flanged male may resist the same male later in the day. Knott et al. (2009) found that females were more resistant toward prime males outside of ovulation. Females that are pregnant or lactating also sometimes resist copulations, despite having no risk of conception. What accounts for this? One possibility is disease avoidance (Fox 2002, Knott and Kahlenberg 2007, Knott 2009). Orangutans at most sites have little physical contact with other members of their species. Females conceive only once every 5–8 years and typically have brief periods of sexual activity during those conceptive periods. Lengthy matings in orangutans and contacts with multiple males during these periods would increase the opportunity for transmission of both macro- and microparasites and disease vectors (Knott 2009). Orangutans have fewer white blood cells than do chimpanzees (Nunn et al. 2000), and thus, their ability to mount an immune response may be lower than that of other primates, perhaps leading them to avoid unnecessary contact.

Eliciting Support from the Dominant Male

van Schaik (2004) argues that females may resist matings with nonpreferred males to elicit the intervention of the dominant male and to convey to the dominant her unwillingness to mate with other males. Data from Tuanan also show that when loud vocalizations were made during a male/female interaction, they were more likely to be terminated by the intervention of another male (van Noordwijk and van Schaik 2009). In many circumstances, though, the dominant male would be too far away to be aware of this interaction. It would also seem to be in the female's interest to prevent the dominant male from being aware of matings with other males in order to increase confidence in his own paternity (Knott 2009).

Avoidance of Energetic Costs

Orangutans may resist some matings in order to avoid the loss of feeding time. Fox (1998) describes a female that showed no resistance to mating with an unflanged male and continued to feed on fruit throughout the mating. However, after 3 min the male grabbed her feeding hand to reposition her, thus preventing her from eating. This was followed by 12 min of struggle between the female and the male. Fox (1998) attributes this female's objection to her need to continue feeding. However, Fox (1998) tested the energetic cost hypothesis but did not find decreased foraging efficiency on days when females had forced consortships. It is also unclear whether female mating resistance would actually lower energetic costs as females are normally not able to prevent an unwanted mating and resistance expends more energy than cooperation. Thus, energetic constraints may explain why females would want to avoid unwanted matings and consortships but does not explain actual resistance during mating.

Decreasing Mating Duration

Resistance is rarely effective. For example, at Kutai, Mitani (1985a) observed females struggling free in less than 10% of forced mating attempts. What benefit might females be gaining from trying to resist copulation, even if resistance is unsuccessful? At Gunung Palung, resisted copulations were shorter in duration than unresisted copulations (Knott et al. 2010). Thus, resistance may serve two possible functions. First, it would reduce the total time of physical contact between the male and female, which may be beneficial for disease avoidance. Second, it may be that orangutans copulate for 8–11 min because it is necessary for ejaculation; thus, it is possible that, by resisting, females can shorten the mating and thus decrease the likelihood of ejaculation (Knott 2009).

Mate Assessment

In some species, females resist mating in order to gain information about the health and vigor of prospective mates (Smuts and Smuts 1993). This possibility may be applicable to orangutans because the sexes have little contact with each other outside of mating. If mate assessment is why orangutan females resist, then stronger, more aggressive males are expected to achieve the highest reproductive success and be chosen by females for their good genes. Fox (1998) predicted that if female resistance was due to mate assessment, females would decrease their resistance to males that had mated aggressively with them in the past, but she did not find support for this hypothesis. However, it may be that mate assessment explains why females often retreat from an advancing male but then become proceptive once contact is made.

Low Costs of Resistance

The cost of resistance must be considered in a female's decision to resist a mating. It is puzzling that females resist copulations given that resistance has been thought to be costly. However, Knott's (2009) recent review of the published data shows, perhaps surprisingly, that there are no reports of females receiving visible wounds from resisted matings. Although forced matings may hurt the female, there is no evidence that they regularly inflict injuries that compromise health or mobility (Knott 2009). Knott (2009) argues that coercion in the mating context in orangutans is direct; that is, males force females to copulate when they resist. They do not appear to use indirect coercion, as has been seen in chimpanzees and humans, where aggression toward females occurs outside of mating to coerce females into mating at a later date (Muller and Wrangham 2009). Thus, females may suffer little physical cost from resisting male mating attempts.

CONCLUSION

Almost 40 years of research on wild orangutans has revealed a range of extraordinary features of their behavior and biology. However, many questions remain unresolved, such as uncovering the mechanism that triggers male development, understanding ranging patterns, and completing genetic and hormonal analyses at multiple sites to understand male and female mating strategies. Many questions, such as juvenile developmental patterns, are just now being addressed and, through the power of long-term data, rare but important behaviors are being revealed, such as female/female aggression and food sharing between adults. Comparative studies have uncovered differences between populations, species, and subspecies (Wich et al. 2009, van Schaik et al. 2009a,b,c). One of the current challenges is to disentangle the sources of this variation. What differences can be attributed to variations in local ecology and, thus, serve as a reflection of phenotypic plasticity? Alternatively, what differences have a genetic foundation reflecting local adaptation? Finally, which behaviors reflects cultural differences between populations? All of these questions deserve our attention; however, the issue that must move to the forefront of all agendas is conservation—habitat protection, in particular—for without increased efforts to save orangutans, we will lose the opportunity to fully understand and appreciate this fascinating great ape.

19

Gorillas

Diversity in Ecology and Behavior

Martha M. Robbins

1. What is the nature of intergroup interactions among gorillas?
2. How do female/female relationships compare to male/female relationships in gorillas?
3. How does male and female dispersal differ among gorillas?

INTRODUCTION

Gorillas are found in 10 central African countries, in a broad diversity of habitats ranging from coastal lowland forests to high-altitude, Afromontane rain forests (Fig. 19.1). The distribution of gorillas makes them a particularly appealing species to study, both in terms of understanding how they have adapted to such a variety of habitats and by providing an excellent opportunity to test many hypotheses of primate behavioral ecology that assume variation in ecology will lead to variation in behavior and demography (e.g., Sterck et al. 1997; *Papio*, Barton et al. 1996; *Presbytis entellus*, Koenig et al. 1998; *Saimiri*, Boinski et al. 2002). However, perhaps one of the biggest ironies of primatology is that the majority of information on gorillas has come from a very small population studied for over 35 years living at a unique ecological extreme (high altitude; Karisoke Research Center, Rwanda). Fortunately, in recent years, several studies of other gorilla populations have begun to provide us with information that is more representative of the genus as a whole, especially on feeding ecology; but because of the difficulty of habituating lowland gorillas, only a limited number of studies involving direct observations have been conducted and much remains unknown. One obvious conclusion, though, is that due to the large differences in ecology between western and eastern gorillas, we can no longer assume that all knowledge of the behavior and demography of mountain gorillas applies to all gorilla populations.

TAXONOMY AND DISTRIBUTION

The taxonomic classification of gorillas has changed many times over the past century (Groves 2003). For much of the past few decades, gorillas were considered only one species with three subspecies (western lowland gorillas, eastern lowland gorillas, and mountain gorillas). A recent taxonomic reclassification now groups gorillas as two species and four subspecies (Groves 2001a) (Fig. 19.1, Table 19.1). Western gorillas include *Gorilla gorilla gorilla* (western lowland gorilla), found in Equatorial Guinea, Gabon, Angola, Cameroon, Central African Republic, and Democratic Republic of Congo, and *G. g. diehli* (Cross River gorilla), found in a handful of small populations in Nigeria and Cameroon. Eastern gorillas (Color Plate 32) include *G. beringei graueri* (eastern lowland or Grauer's gorilla), found in the east Democratic Republic of Congo, and *G. b. beringei* (mountain gorilla), found in two small populations at the Virunga Volcanoes of Rwanda, Uganda, and Democratic Republic of Congo and in the Bwindi Impenetrable National Park of Uganda (Figs. 19.2 and 19.3). Genetic studies suggest that the initial split between eastern