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Orangutan Behavior and Ecology

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The striking orangutan, the red ape of Asia, has intrigued scientists from the days of nineteenth-century explorers like Alfred Russell Wallace. However, as recently as 1965, George Schaller wrote that "there have been no field studies of the orangutan." This situation has changed dramatically over the intervening years. Many long- and short-term studies on orangutan behavior and ecology have now been conducted in the wild. Through these investigations we have found that orangutans are extreme or unusual among primates in a number of fascinating ways. They are the most solitary, have the longest interbirth intervals, display an unusually high degree of forced copulation, and adult males may possibly come in two different morphological types. However, orangutans still remain difficult to study due to their predominantly solitary nature and the often difficult to access habitats where they are found. Much still remains unknown or unexplained. In this essay I will briefly review the literature regarding orangutan ecology and behavior, highlighting some of the newest findings from my own research in Gunung Palung National Park in Western Borneo, as well as recent studies in Suaq Balimbing Forest and Ketambe Forest in Gunung Leuser National Park, Sumatra.

Orangutans may best be understood by placing them within their ecological context, that is, by studying how the environment in which they are found has shaped their evolution and continues to influence their behavior and physiology. This approach helps us to move beyond description and begin to understand *why* certain behaviors are observed. To answer these questions in orangutans, as well as other primates, we now have some new tools: hormonal measurements, nutritional biochemistry, urinalysis, and genetic studies. These techniques provide noninvasive ways to test hypotheses about behavior and physiology that have not been possible before in the wild. Working within an ecological framework, these new techniques allow us to study the "ecophysiology" of wild primates and to investigate what determines survival and reproduction—the key elements of evolution.

TAXONOMY AND DISTRIBUTION

Orangutan literally means "person of the forest" in the Malaysian and Indonesian languages spoken in the countries where orangutans are found. Currently, orangutans are restricted to the islands of Borneo and Sumatra, although during the Pleistocene they were more widespread across Southeast Asia (MacKinnon 1971). Orangutans from the two islands are normally divided into two separate subspecies: *Pongo pygmaeus pygmaeus,* from Borneo, and *Pongo pygmaeus abelii,* from Sumatra. Bornean and Sumatran orangutans are quite behaviorally and morphologically similar, but there is a higher degree of genetic difference between them than is found within other great ape species (Caccone and Powell 1989; Ruvolo et al. 1995; Lu et al. 1996; Uchida 1996). This genetic difference has led some to suggest that the two subspecies should be separated into two species (Ryder and Chemnick 1993).

However, there is a lack of general agreement about the degree of genetic difference that justifies a species level distinction (Jolly, Oates, and Disotell 1995), and in captivity Bornean and Sumatran orangutans can easily interbreed and produce fertile offspring (Muir, Galdikas, and Beckenbach 1995).

ENVIRONMENT

Orangutans live in rain forest habitats ranging from sea-level swamp forests to mountain slopes rarely exceeding 1200 m (Djojosudharmo and van Schaik 1992). These forests are true wet, rain forests with average rainfall ranging from slightly over 2000 mm per year (Galdikas 1988) to 4500 mm per year (Lawrence and Leighton 1996), depending on the site and year sampled. One of the principal orangutan habitats is forest dominated by the large trees of the *Dipterocarpaceae* family. This type of forest is characterized by "mast fruitings," a phenomenon that occurs approximately every two to ten years (Ashton, Givinish, and Appanah 1998) in which up to 88% of rain forest tree species may fruit at the same time (Medway 1972; Appanah 1986; van Schaik 1986). This fruiting pattern is unique to the rain forests of Southeast Asia (Janzen 1974). Some orangutan habitats, such as peat swamp forests, do not exhibit mast fruiting, but fruit production is still highly variable (Galdikas 1988). Although African and South American rain forests also have fluctuations in fruit availability, Asian forests in general are characterized by more temporal and spatial variability in fruit production (Fleming, Breitwisch, and Whitesides 1987). This causes dramatic fluctuations in the type and quantity of fruit available to orangutans (Knott 1998a). This resource unpredictability may help us explain many of the unique aspects of orangutan physiology and biology.

GENERAL DESCRIPTION

Orangutans are the largest of all canopy animals with wild adult males weighing 86.3 kg on average and females 38.5 kg (Markham and Groves 1990). Such large animals move through the canopy by **quadrumanual clambering** (using all four hands and feet to grasp and pull themselves along) and occasional brachiation (particularly by smaller individuals). They also effectively use their body weight to bend and sway small trees, using the stored momentum in the tree as a spring to propel themselves across a gap until they can grasp an adjacent branch.

Compared to humans and other great apes, the orangutan's arms, hands, and feet are extremely long (Fleagle 1988). Their shallow hip joint permits them to extend their legs by more than 90 degrees (MacLatchy 1996), allowing them to hang suspended by any hand-foot combination. These features help them contort their bodies into unusual positions to reach hard to access fruit and to negotiate their way through the rain forest canopy where they spend almost their entire lives. Orangutans rarely descend to the ground, although adult males do so more often than females (Rodman and Mitani 1987). This sex difference in ground locomotion may be due to constraints posed by canopy travel on adult males (Rodman and Mitani 1987), or, alternatively, females with offspring may be more vulnerable to the occasional ground predator (Rodman and Mitani 1987; Setiawan, Knott, and Budhi 1996).

Female orangutans are less than half the size (approximately 45%) of developed adult males (Markham and Groves 1990). This is one of the highest degrees of sexual dimorphism seen in primates. The ultimate causes of this sexual dimorphism have been attributed to male-male competition (Rodman and Mitani 1987), female choice (Fox 1998), and sexual coercion (Smuts and Smuts 1993). All may have been important in the evolution of large male body size in orangutans. Female orangutans are considered to be the "ecological" sex, that is, to exhibit a body size that is primarily constrained by nutritional factors rather than competition (Demment 1983; Rodman and Mitani 1987).

Fully adult males are also striking for their secondary sexual characteristics, such as the production of the long call and their projecting cheek "pads." Experiments indicate that the loud, bellowing long calls seem to function primarily to mediate spacing between males (Mitani 1985a). The production of and response to long calls varies depending on dominance (Mitani 1985a; Utami and Setia 1995). Further studies of receptive females are needed to adequately test whether females also respond to male long calls (Mitani 1985a). The jutting cheek pads of adult males are composed of fibrous fatty tissue (Winkler 1989) and are one of the most unusual features of the orangutan's appearance. It has been speculated that they seem to help locate (Galdikas 1983) or concentrate the sound of a long call (Rodman and Mitani 1987). However, an alternative explanation may be that these cheek pads have evolved because they help increase the male's apparent size. There has been strong selection for large body size in adult male orangutans (Rodman and Mitani 1987), but males may not have been able to evolve any bigger and still maintain their primarily arboreal lifestyle. Selection may instead have operated to increase the width of the face and, thus, the apparent overall size of the animal.

Intriguingly, it has been proposed that there may be two types of fully "adult" males (Kingsley 1982, 1988; Schürmann and van Hooff 1986; te Boekhorst, Schürmann, and Sugardjito 1990; Graham and Nadler 1990; Maggioncalda 1995b) with one type, which I will call "developed" males, exhibiting the large male body size and secondary sexual characteristics I have described, and the other, "undeveloped" males, retaining a smaller, "subadult" size morphology. Some of these small males may just be in transition before full maturation. Other males seem to remain longer in an undeveloped stage. Males have been reported to still be "subadults" at an estimated age of twenty years in the wild (Schürmann and van Hooff 1986) and up to eighteen years in captivity (Kingsley 1988). Studies of orangutan skulls have shown that there are males whose cranial sutures have closed, although they remain small (Uchida 1996). Thus, it appears that the timing of development of secondary sexual characteristics may occur within a broad age range in orangutan males, anywhere between ten and twenty years of age, and that males may remain undeveloped for ten years or longer (Kingsley 1988; Schürmann and van Hooff 1986). Review of the literature indicates that all males, however, do eventually develop secondary sexual characteristics; there are no known individuals from zoos or in captivity that have remained undeveloped beyond twenty years.

Males who remain undeveloped for an extended period have significantly lower levels of testosterone (Kingsley 1982; Maggioncalda 1995a) and growth hormones (Maggioncalda 1995a) than do males who are in the process of developing. However, these undeveloped males appear to have adequate production of testosterone and are fully capable of fathering offspring (Kingsley 1982, 1988). Interestingly, testosterone levels were significantly higher in developing males than in fully developed males in captivity (Maggioncalda 1995a) as well as in the wild (Knott 1997b). Kingsley (1982) did not find this difference in captivity, but her sample was limited to two developing males.

What triggers the timing of full development in males? It has been proposed that the presence of a developed adult male may "suppress" maturation in undeveloped males (Kingsley 1982; Schürmann and van Hooff 1986; Maggioncalda 1995b). This is based on inferences from captivity in which some undeveloped males mature soon after they are separated from their developed cagemates. These correlations, however, do not rule out the possibility that such males would have matured at that time regardless of the presence of a developed male. Males are also seen to develop cheek pads while still in the presence of an already developed male (Kingsley 1982). It is also difficult to imagine how an inhibitory mechanism could operate in the wild where orangutan males are rarely within visual or olfactory contact. Maggioncalda (1995b) suggests that undeveloped males may use long calls to monitor the density of developed males as a cue for when to initiate full maturation. However, not all developed males regularly produce long calls (Utami and Setia 1995; Knott, pers. obser.). Thus, long calls are not an accurate indicator of density. Alternatively, differing ages of maturation in adult males may result from changes in energetic status brought about by fluctuating nutrition, or males may simply vary genetically in their developmental timetables.

ACTIVITY PATTERNS

The time orangutans spend in different activities varies depending on the availability of food, social conditions, and reproductive status. Averaging across three studies (MacKinnon 1974; Rodman 1979a; Mitani 1989), orangutans spend approximately 44% of their time resting, 41% feeding, 13% traveling, 2% nest building, and less than 1% engaging in other activities, such as fighting, mating, and socializing. These percentages may, however, vary tremendously. Because orangutans are primarily solitary, their activity patterns may be very individualistic. Each animal may react in a different way to the same environmental conditions. For example, during periods of low fruit availability, I have found that some individuals will travel between habitats, expending more energy than during periods of high fruit availability to search out the few species that are fruiting, whereas other individuals may severely limit their foraging time and maintain their body reserves (Knott 1998c). An individual's condition, reproductive status, and territory quality may influence these decisions.

FEEDING ECOLOGY

The orangutan diet varies dramatically depending on what foods are available. Fruit, both pulp and seeds, is the preferred food of orangutans (e.g., Sugardjito, te Boekhorst, and van Hooff 1987; Galdikas 1988; Leighton 1993). Orangutans prefer to feed in trees with large patches of fruit when it is available (Leighton 1993). Sugardjito (1986) found that adult males have longer feeding bouts than do adult females, and Rodman (1979a) noted that males tend to feed in fewer food patches per day than do females. When fruit is abundant, such as during a mast fruiting, the orangutan diet may consist of 100% fruit (Knott 1998a). However, during fruit poor times, orangutans must rely on more abundant, but relatively lower quality, food such as the inner cambium layer of bark, leaves, pithy plants, and insects. During a several month period of particularly poor fruit availability following a mast fruiting, I found that orangutans at Gunung Palung ate 37% bark, 25% leaves, 21% fruit, 10% pith, and 7% insects (Knott 1998a).

These changes in dietary composition also result in dramatic differences in nutritional intake. During a period of high fruit availability, orangutans at Gunung Palung were able to obtain an average of 8422 Kcal/day for males and 7404 Kcal/day for females, whereas during periods of low fruit availability, their caloric intake decreased dramatically to 3824 Kcal/day for males and 1793 Kcal/day for females (Knott 1998a). These differences were primarily due to the increased nutritional and caloric content of foods available during these two periods. During the mast period of high fruit availability, fruits most commonly eaten by orangutans were significantly higher in caloric content as well as in lipids and carbohydrates than were foods eaten during the low fruit period (Knott 1999).

Orangutans have been seen to eat meat only on rare occasions. In Sumatra, three adult females have been observed on seven occasions to hunt and eat slow lorises (*Nycticebus coucang*) (Utami 1997), and one female was observed to eat a gibbon (Sugardjito and Nurhada 1981). At Gunung Palung in Borneo I've witnessed a juvenile female orangutan catch and eat a rat (Knott 1998b). Thus, the ability to capture other mammalian prey may be a relatively ancient ability in hominoids as it is also observed in chimpanzees (e.g., Teleki 1973; Goodall 1986; Boesch and Boesch 1989; Stanford et al. 1994), and bonobos (Ihobe 1992a).

ENERGY BALANCE

Orangutans seem to have a pronounced ability to store excess food resources as fat (Wheatley 1982, 1987; Leighton 1993; Knott 1998a). In captivity, in fact, they have a greater tendency toward obesity than do other great apes (MacKinnon 1971). These dramatic fluctuations in caloric and nutritional intake may have serious consequences for orangutan physiology and energy balance. During periods of low fruit availability, I have found that orangutans burn up their own fat deposits to utilize as energy (Knott 1998a). When caloric intake is particularly low, they may start producing "ketone bodies," which are products of fat metabolism and can be detected in urine using single dipstick tests (Knott 1997a, 1998a). These fluctuations in fruit availability provide orangutans with the *opportunity* to store excess energy as fat, which they can then utilize during fruit poor times.

SOCIAL SYSTEM AND RANGING PATTERNS

The orangutan social system has been difficult to characterize because these animals often range over extensive areas and their residence in a given study area may vary widely across time. Mounting evidence suggests that females tend to stay in their natal area, whereas males disperse (Rodman 1973; Rijksen 1978; Galdikas 1988; Knott, pers. obser.). Horr (1975) and Rodman (1973) saw little overlap in female ranges, but longer term studies (Galdikas 1988; van Schaik and van Hooff 1996; Utami 1997; Knott 1998c) have found that female ranges can overlap considerably.

Developed adult males can have overlapping ranges, with the number of developed males using a given area at the same time ranging from one (Rodman 1973) to as many as six (Knott 1998c, 1999). Some males may stay resident in an area, whereas others appear to be transient. However, this may be a false distinction (van Schaik and van Hooff 1996) as the researcher's perception of residence patterns may depend on the length of time sampled and the inability to know where individuals are when they are not in the core study area. At Gunung Palung, these differences in male ranging patterns seem to be tied to fluctuations in fruit availability, with more males using the study area during periods of high fruit availability (Knott 1998c).

Thus, developed males appear to have large and widely overlapping ranges within which they search for receptive females. This evidence suggests that the orangutan social system can best be characterized as "roving male promiscuity" in which "males cannot defend access to female ranges and females do not congregate at particular areas" (van Schaik and van Hooff 1996). Small, undeveloped males, however, are often seen to travel in groups and to corral females for mating. Thus, undeveloped males practice a form of roving male promiscuity wherein they sometimes form associations, whereas developed males never do. Genetic data will help us resolve some of the long-standing questions regarding relatedness between individuals within an orangutan population as well as the relative paternity success of developed versus undeveloped males.

SOCIAL BEHAVIOR

Why do orangutans differ so much from the gregarious nature of most other primates? Why don't adult males bond together to defend female home ranges from other males? The answer may lie in the comparison between the ecology of orangutans living in Asian rain forests and the ecology of the more convivial African apes. It has been suggested that orangutan fruit trees are more widely dispersed compared to African fruit trees (Fleming et al. 1987). However, no systematic studies have been done comparing ecological differences between these different rain forests as they might relate to great apes. It appears, though, that fruit trees preferred by orangutans in Asian rain forests are significantly smaller in diameter compared to those used by chimpanzees and bonobos (Knott 1999). Thus, the scarcity of large patches of fruit may limit the ability of orangutans to forage together as a group.

Examining the occasions when orangutans *are* social can help us understand why they are usually solitary. Aggregations of orangutans have been found in large fig trees (MacKinnon 1974; Rijksen 1978; Sugardjito et al. 1987), in large dipterocarp trees that only fruit during mast fruitings (Knott 1998c), and other times when closely packed trees, such as *Palaquium* are fruiting (Knott 1998c). These aggregations are primarily composed of mothers with offspring, undeveloped males, and an occasional lone developed male. During periods of increased sociability, orangutans may modify their time spent feeding (MacKinnon 1974; Rodman 1977; Galdikas 1988; Mitani 1989), traveling (Galdikas 1988; Mitani 1989; Knott 1998c), and resting (Mitani 1989). Costs of grouping may constrain group travel of orangutans except during exceptional periods when the nature and distribution of fruit resources permits it. Increased sociability (Knott 1998c) and density (te Boekhorst et al. 1990) have been strongly correlated with periods of high fruit availability. Furthermore, some orangutan populations may not be as solitary as was once thought. In Suaq Balimbing forest in Ketambe, van Schaik and Fox (pers. comm.) have found that orangutans are much more social than has previously been described at other sites.

Another cause of grouping, the risk of predation, appears to be not very important for orangutans given their large body size (Sugardjito 1983; Setiawan et al. 1996). Because individuals rarely form groups, threats by groups of orangutans directed at lone individuals have not been observed except in the case of forced matings. Lethal aggression does occur in orangutans, particularly between developed adult males, but this threat does not lead to the formation of bonds between developed males. Undeveloped males, however, may form bonds as a response to threats from developed males and as a way to gain group access to cycling females.

REPRODUCTION AND LIFE HISTORY VARIABLES

Like humans, orangutans have no estrus swellings and no visual indicators of ovulation (Schultz 1938; Graham-Jones and Hill 1962), and the orangutan menstrual cycle has a mean length of 28 days (Nadler 1988; Markham 1990). Females reach sexual maturity at approximately eleven to fifteen years in the wild (Galdikas 1981), although maturation can occur as early as seven to nine years in captivity (Asano 1967; Masters and Markham 1991). The ability of females to conceive is also reduced during adolescence (Schürmann and van Hooff 1986; Galdikas 1995). Sexual maturation in males ranges broadly. Males have been known to father offspring as early as 6.5 years in captivity (Kingsley 1982). The transition from an adolescent to an undeveloped adult male stage occurs at approximately seven to ten years of age (Graham and Nadler 1990). After that, as explained previously, full development may proceed directly or may be delayed for ten years or more (te Boekhorst et al. 1990). Average completed orangutan life span in the wild is not known, but captive individuals have lived into their late fifties (Bond, National Orangutan Studbook Keeper, pers. comm.).

Orangutans have been reported to have an average completed interbirth interval of eight years—the longest of any primate and indeed one of the longest in any mammal (Galdikas and Wood 1990; Tilson et al. 1993). This interbirth interval ranges between 5.9 years and 10.4 years at Tanjung Puting in Central Borneo where orangutans have been studied the longest (Galdikas and Wood 1990). Infants and juveniles nurse for approximately six years (Galdikas 1980), during which time female hormonal levels appear to be suppressed (Knott 1999). The length of gestation is approximately eight months (Markham 1990).

What causes this long interbirth interval in orangutans? In my study, I have shown that hormonal levels respond to changes in energetic status brought about by fluctuations in fruit availability. During periods of high fruit availability, orangutans have significantly higher levels of urinary estrogens than during periods of low fruit availability (Knott 1997a, 1999). Thus, when times are poor, orangutans may find it more difficult to conceive, lengthening the interbirth interval. Given that a period of fruit abundance may come along only once every few years in the Southeast Asian rain forest, it may be difficult for orangutans to reproduce more quickly. This is supported by examining captive orangutans, wherein dramatically reduced energy expenditure and increased caloric intake compared to the wild are associated with much faster reproductive parameters. Captive orangutans reach sexual maturity earlier (Masters and Markham 1991), conceive sooner after giving birth (Lasley, Presley, and Czekala 1980), and have shorter interbirth intervals (Markham 1990) than wild orangutans. Low body weight in captivity has also been associated with amenorrhea, and weight gain has been shown to increase urinary hormonal levels (Masters and Markham 1991).

SOCIOSEXUAL BEHAVIOR

A surprisingly large percentage of orangutan matings have been characterized as forced copulations (MacKinnon 1974; Rijksen 1978; Galdikas 1981, 1985a; Mitani 1985b). In the wild, undeveloped males appear to engage in more forced copulations (Schürmann 1982; Rodman and Mitani 1987) and, usually, more copulations in general than do fully developed males (MacKinnon 1974; Rodman and Mitani 1987). However, both developed and undeveloped males can and do force females to copulate (Mitani 1985b). Orangutan females, due to their mostly solitary ranging patterns, may be particularly vulnerable to this type of sexual coercion compared to other primates (Smuts and Smuts 1993). Whether females *choose* to mate with developed males or whether they cooperate due to threat of injury from these large males is not well understood. Fox (1998) found that females showed active mate choice. Nadler (1977) looked at the relationship between the female hormonal cycle and mating in captive orangutans and found that when male access to the female was not limited copulations occurred on a nearly daily basis. However, during the midcycle period, female resistance to males was lower, and multiple copulations occurred more frequently. In later experiments, when females were allowed to *choose* when to enter a male's cage, mating was limited to midcycle (Nadler 1988). Current studies are examining the relationship between the menstrual cycle and reproductive activity in the wild (Fox 1998; Knott 1999). In my study, I have found that matings are much more common during periods of high fruit availability when urinary estrogen levels are higher in females (Knott 1997b).

ORANGUTAN COGNITIVE ABILITIES AND TOOL USE

Orangutans in captivity have been found to be highly intelligent, habitually making and using tools (Lethmate 1982). Orangutans raised in people's homes and later brought to rehabilitation centers have been taught sign language (Shapiro and Galdikas 1995) and regularly emulate human activities (Russon and Galdikas 1995). It has thus been surprising that almost no reports have been made of habitual tool-using behavior in wild orangutans. However, new evidence of tool use in the wild is now emerging. Van Schaik and Fox (1996) report from the recently established site at Suaq Balimbing in Sumatra that orangutans regularly use tools to extract seeds from *Neesia* fruits as well as to access insects from tree holes. Stick tools of specified lengths are made for each of these tasks. This behavior is not explained by simple availability of foods, as orangutans at Gunung Palung also eat *Neesia* but do not use tools to extract them (van Schaik and Knott 1998). The greater density of orangutans at Suaq Balimbing, perhaps due to increased fruit availability, may have allowed for more social encounters than at Gunung Palung and more opportunities for transmission of cultural information.

Other tool-using behaviors are also observed in the wild. Orangutans regularly make leaf umbrellas to cover themselves during heavy downpours and use branches in agonistic displays (MacKinnon 1974; Rijksen 1978; Galdikas 1982; Knott, pers. obser.). Occasional observations have been made of orangutans using leaves for self-cleaning (MacKinnon 1974; Rijksen 1978) and as protection in food acquisition (Rijksen 1978), dead wood for opening up durian fruits (Rijksen 1978), and sticks for scratching (Galdikas 1982). At Gunung Palung we have recently witnessed orangutans using leaves as drinking tools. Although these behaviors may remain rarer in orangutans than in chimpanzees, they demonstrate that orangutans *do* have the capacity for tool use in the wild and, like chimpanzees (McGrew 1992), there may be population or "cultural" differences in tool usage.

CONSERVATION STATUS

Orangutans are internationally recognized as endangered species. Their rain forest habitat has declined by more than 80% over the past twenty years due to timber extraction and conversion of rain forest for plantations and agriculture (Tilson et al. 1993). This, augmented by hunting orangutans for meat and killing adult females to obtain infants for the illegal pet trade, has resulted in an estimated decline in the orangutan population of 30 to 50% over the past ten years. Uncontrolled forest fires have also destroyed significant portions of orangutan habitat in both Sumatra and Borneo. The continued survival of the orangutan is in significant peril. Only through concerted efforts to preserve orangutan habitat and prevent continued hunting of individuals can we hope to sustain populations of wild orangutans into the twenty-first century.

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