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 extremely 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 mate in two different morphological types. However, orangutans still remain difficult to study due to their predominantly solitary nature and the difficult 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 latest findings from my own research in Gunung Palung National Park in Western Borneo, as well as recent studies in Suau Balikmu 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 descriptions 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 innovative 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 “ecophenotypes” of wild primates and to investigate what determines survival and reproduction—the key elements of evolution.

**TAXONOMY AND DISTRIBUTION**

Orangutans literally means “person of the forest” in the Malay and Indonesian languages spoken in the countries where orangutans are found. Currently, orangutans are restricted to the islands of Borneo and Sumatra, although Jutting 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. 1993; Liu et al. 1996; Uchida 1996). This genetic difference has led some to suggest that the two subspecies should be separated into two species (Byrd and Cheennick 1993)

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

**ENVIRONMENT**

Orangutans live in rain forest habitats ranging from sea-level swamp forests to mountain slopes rarely exceeding 1200 m (Dyosojadharma and van Schaik 1992). These forests are true wet, rain forests with average rainfall ranging from slightly over 2000 mm per year (Galikas 1988) to 4500 mm per year (Lawrence and Leighton 1990), depending on the site and year sampled. One of the principal orangutan habitats is forest dominated by the large trees of the Dipterocarpus family. This type of forest is characterized by “mast fruitions,” a phenomenon that occurs approximately every two to ten years (Ashkin, Givnish, and Appah 1998) in which up to 88% of rain forest tree species may fruit at the same time (McShea 1972, Appah 1986, van Schaik 1986). This fructiferous 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 (Galikas 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 Whithney 1987). This causes dramatic fluctuations in the type and quantity of fruit available to orangutans (Knot 1990b). 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 grab and pull themselves along) and occasional banchiation (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. These small hip joint permits them to extend their legs by more than 90 degrees (DacLatchi 1990), allowing them to hang suspended by any hand-foot combination. These features help them contest their bodies into unusual postures 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 Mittani 1987). This sex difference in ground locomotion may be due to constraints posed by canopy travel on adult males (Rodman and Mittani 1987), or, alternatively, females with offspring may be more vulnerable to the occasional ground predator (Rodman and Mittani 1987; Setiawan, Knot, and Budih 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 Mittani 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 Mittani 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...
the literature indicates that all males, however, do eventually develop secondary sexual characteristics. There are no known reports from 1988 or in captivity that have remained undeveloped beyond twenty years.

Males who remain undeveloped for an extended period have significantly lower levels of testosterone (Kingley 1982; Maggioncalda 1996a) 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 (Kingley 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 (Knot 1997b). Kingley (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 timing of a developed adult male may "suppress" maturation in undeveloped males (Kingley 1982; Schirman and van Hoof 1986; Maggioncalda 1995b). This is based on inferences from captive in which some undeveloped males matured 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 check pads while still in the presence of an already developed male (Kingley 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; Knot, pers. obs.). 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; Miti and Miti 1988), orangutans spend approximately 44% of their time resting, 41% feeding, 13% traveling, 2% next 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 fructing, whereas other individuals may simply limit their foraging time and maintain their body reserves (Knot 1998c). An individual 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 and Northbail 1981). At Gunung Palung I've witnessed a juvenile female orangutan catch and eat a rat (Knot 1998a). 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., Teieki 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 (Whetley 1982, 1987; Leighton 1993; Knot 1998b). In captivity, in fact, they have a greater tendency toward obesity than do other great apes (MacKinnon 1971). These dramatic fluctuations in caloric 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 (Knot 1998a). When caloric intake is particularly low, they may begin producing ketone
bodies,” which are products of fat metabolism and can be detected in urine using single dipstick tests (Knot 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; Galikas 1988; Knot, pers. obs.). Horst (1975) and Rodman (1973) saw little overlap in female ranges, but longer term studies (Galikas 1988; van Schaik and van Hooff 1990; Utsui 1997; Knot 1998c) have found that female ranges can overlap considerably.

Developed adults 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 (Knot 1998b, 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 1990) 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 (Knot 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 1990). Small, undeveloped males, however, are often seen to travel in groups to and from females. These are probably individuals who have never participated in 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 thegregarious nature of most other primates? Why don’t adult males bond together to defend female home ranges from other males? The answer may be in the comparison between the ecology of orangutans living in Asian rain forests and the ecology of the more carnivorous 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 the fruit trees preferred by orangutans in Asian rain forests are significantly smaller in diameter compared to those used by chimpanzees and bonobos (Knot 1990). 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 fruitions (Knot 1998b), and other times when closely packed trees, such as Palasium are fruiting (Knot 1998c). These aggregations are primarily composed of mothers with offspring, undeveloped males, and an occasional low developed male. During periods of increased sociability, orangutans may modify their time spent feeding (MacKinnon 1974; Rodman 1977; Galikas 1988, 1990; Komog (Galikas 1988); Iwamoto 1989; Knot 1998c), and tend to group together in the presence of food (Iwamoto 1989).

**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 15 years in the wild (Galikas 1980), although menstruation 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 (Schirrmann and van Hooff 1986; Galikas 1993). Sexual maturation in males ranges broadly. Males have been known to father offspring as early as 6.5 years in captivity (Kingsley 1984). The transition from an adolescent to an undeveloped adult male stage occurs at approximately 15 years in the wild (Galikas 1988). 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 (Knot 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 Suau Balansiling forest in K etambe, 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. 1990). 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 between 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.
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 (Schimmann 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 1993) and regularly emulate human activities (Russon and Galdikas 1995). It has 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 Suau Bambang in Sumatra that orangutans regularly use tools to extract seeds from Neesia fruits as well as to access insects from tree holes. Sticks 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 Suau Bambang, 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. obs.). 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 detangling 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 populations 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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