

ORANGUTAN BEHAVIOR

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INTRODUCTION

It has often been said that wild orangutans are enigmatic due to their perceived solitary nature and the fact that there still appear to be no easily recognisable social units. They are also unusual in many other ways. For instance, they exhibit an unusually high degree of sexual dimorphism, are very large for an arboreal animal (in fact they are the largest arboreal mammal), possess the longest inter-birth of any land-based mammal, display an unusually high degree of forced copulation, and sexually mature males appear to come in two distinct morphological types, each with its own mating strategy. However, new information has also come to the fore as a result of research in previously unstudied areas and examining previously unstudied aspects of their behavioural ecology. This article is an attempt to present some of what we know about orangutan behaviour in both wild and captive settings and to summarize some of these recent findings, particularly where they may be relevant to how the species is managed in captivity.

RECENT DISCOVERIES

Tool use

One of the most significant findings is that of tool use among wild orangutans in the swamp forests of the west coast of northern Sumatra. Zoo people have long been aware of the cognitive and dextrous ability of the orangutan but this was never backed up by similar observations in the wild until the establishment of the Suaq Balimbing research station in South Aceh, Sumatra. Here orangutans routinely make and use tools on an almost daily basis (see Fox *et. al.* 1999, van Schaik *et. al.* 1999). Tools take the form of simple sticks, used to extract honey from bees nests and seeds from the fruits of the Neesia tree. Encased in an extremely hard casing, this fruit splits open in a few places and the seeds are located inside, surrounded by thousands of tiny needle-like hairs that penetrate the skin of anyone (or anything) trying to obtain them. The orangutans often fray the end of the sticks using their teeth, especially if extracting honey and other insect products from holes in trees. What is particularly interesting about this tool use is the fact that it doesn't occur outside of the Sumatran swamp forests. Even in other parts of Sumatra, where honey is readily available in bees nests, tool use has still not been observed in truly wild orangutans (though of course rehabilitants seem almost as adept as their zoo counterparts in this respect). The difference appears to be the social setting. At Suaq, where orangutan densities are unusually high and orangutans encounter each other on a daily basis, even spending several days travelling together. Thus opportunities for social learning (see below) are much greater than among their more dispersed low hill forest neighbours and among even the swamp dwelling orangutans of Borneo, where densities also tend to be distinctly lower than in similar habitats in Sumatra.

Orangutan 'cultures'

The relatively recently observed tool use in the wild has recently been examined along with other known wild orangutan behaviours in different study sites in an attempt to determine whether there is evidence for orangutan 'culture' (van Schaik *et. al.* in press). In this context culture can be somewhat simply defined as 'local traditions and behaviours that one population does but that another doesn't do, or does differently, for no obvious ecological reason other than simply that they have learned things differently'. The existence of human cultures has often been proffered as the major feature of human societies that distinguishes them from the rest of the animal kingdom. In the past, tool use has also been proffered but since the first wild chimpanzees were found routinely making and using tools some decades ago many anthropologists have resorted to 'culture'. Previous work looking at the evidence for culture among chimpanzees, however, shows that the evidence for its existence among animal societies is overwhelming (Whitten *et. al.* 1999). It now seems that the evidence for culture among orangutans is similarly very convincing. As an example, the tool use mentioned above is present in all swamp populations of orangutans on the west coast of Sumatra, north of the Simpang Kiri/Alas River. South of this river, however, in exactly the same habitat type and with comparable orangutan densities, the behaviour is absent. This therefore suggests that it simply hasn't been invented there yet, or if it has, the sociality of the orangutans there may be less, so they don't have as much opportunity to learn the behaviour from their peers. Unless a 'new' behaviour is witnessed and learned by other individuals (e.g. if densities are much lower and/or associations between individuals are much less common), then any 'invented' behaviour will subsequently go extinct when the 'inventor' dies. Thus, as mentioned, it seems there are local traditions and behaviours among different populations of orangutans, and hence cultures, just as there are with chimpanzees and humans.

Another interesting and amusing example of this is regional differences in the behaviour of orangutans when they emit the 'kiss-squeak' vocalisation. At Suag Balimbing (west coast swamp forest in Sumatra) they simply make the noise with their lips. At Ketambe (further east in Sumatra; dry foothill forests) they often hold their hands, balled into a fist shape, in front of their lips when they do it. In Gunung Palung (West Borneo) they even grab leaves from a nearby branch and hold them in front of their lips to do it, then let the leaf drop to the ground once the sound is made. These variations in techniques appear somewhat bizarre as the fist balling, and leaf dropping seem to serve no purpose in making the call itself. Nor do they seem to amplify the sound or alter it in any way. This therefore represents another example of cultural differences between orangutan populations.

CURRENT STATE OF KNOWLEDGE

Home ranges

Orangutan home ranges are large, but at least for most, appear to be stable over time. Studies are now showing that ranges of all age sex classes are distinctly larger than estimates made by some of the early researchers (e.g. Horr 1975, 1977, Rodman 1988, Mitani 1989, Suzuki 1992, Rijksen 1978). In fact, baseline

data suggests that adult females occupy core areas (in which they are normally found) of ca 8 km², but that they possess larger ranges, reaching as much as 15 km², whose peripheries they visit according to fruit availability there (Singleton and van Schaik 2001). For both adult (flanged) males and subadult (non-flanged) males we still do not know the true extent of their ranges but we can safely conclude that they are at least in excess of 30 km² and probably much more (Singleton and van Schaik 2001). Nevertheless, as stated, even the males tend to return to study sites eventually, which again suggests large but limited ranges as opposed to individuals simply wandering at random over the landscape.

Looking at female ranges alone, it is also generally easy to plot the limits to their ranges on a yearly basis and see that there are some areas that they simply never go, as they are not included within their range boundaries. Even when fruit has been seen to be exceptionally abundant just a short distance from a female's range boundary she will not go there if it is outside of her range. Such boundaries are remarkably consistent over time, meaning that they are reluctant to venture outside of their ranges and hence unlikely to move readily if the forests within them are damaged (see Singleton 2000, Singleton and van Schaik 2001). Recent studies do tend to concur with the older ones (e.g. Galdikas 1988), however, in that it is the females that settle in ranges overlapping or near to those of their mothers and the males that disperse over greater distances, probably during the subadult or non-flanged phase (e.g. Galdikas 1988, Leighton and Leighton 1983).

Ranges of all age and sex classes also overlap. In some areas the degree of overlap is considerable. At Suaq Balimbing, choosing a single 4 ha location within the study area, it was possible to see that at least 16 adult females, 9 adult males and at least 15 (but probably more likely around 30 or so) unflanged males included that location within their ranges (Singleton 2000).

As mentioned, the above range sizes tend to differ somewhat from much of what has been published previously. However, there are good reasons to believe that most previous studies have significantly underestimated the range sizes of their study animals. For example, some simply assumed that their study animals didn't venture far outside the study area based on the fact that they often found these animals within it. On the other hand these findings are remarkably consistent with those of Galdikas in Tanjung Puting who also reported very large ranges (Galdikas 1988).

Trying to replicate such vast ranges for captive animals is of course impossible for most zoos, at least for the time being! However, it does reinforce the fact that captive orangutans need both stimulation and exercise. Generally the more novel experiences and challenges they can be offered the better so behavioural enrichment efforts should be diligently maintained and efforts to find new ways of stimulating the animals should be continuously sought.

Range use and diet

Wild orangutans utilise different parts of their large home ranges according to both spatial and seasonal variation in food availability. For example, forests vary in the local density of tree species and orangutans tend to go to the area where

a preferred tree species is in fruit at the highest densities (Singleton 2000). Some parts of their ranges may be normally used only when fruit is generally scarce everywhere (e.g. if they offer more varied supplies of leaves, bark and insects). Thus there is localised variation in home range use and it has been speculated in the past that there is seasonal migration (e.g. MacKinnon 1974, Rijksen and Meijaard 1999). However, it is beginning to seem that migration as such, does not occur, and instead, that individual orangutans simply move around within very large, but nonetheless 'fixed' home ranges (see Singleton and van Schaik 2001).

Orangutans begin moving through the forest at daybreak and spend a large part of their day foraging for food. They normally make a new sleeping nest each evening but will on occasions re-build or re-use an already existing nest. In many areas they also normally make a nest to rest in during the day, around noon but this is far more common in Sumatra than in Borneo. Nests are constructed in the trees by bending branches and weaving a loosely formed "bowl" lined with leaves and twigs. Sometimes the animals cover themselves with additional foliage once inside the nest, either for protection from rain or the sun.

Habitat of wild orangutans includes a variety of forest types, with the highest population densities found in swamp forests and lowland hill forests (dipterocarp) and lower population densities found in higher altitude hill and montane forests (Schaller 1961; Horr 1975; Rijksen 1978, van Schaik *et. al.* 1995). Densities also appear to be generally higher in Sumatra than in Borneo, in similar habitat types (van Schaik *et. al.* 1995; Delgado and van Schaik 2000). The diet of wild orangutans is varied, but fruits are preferred food items, generally constituting around 60% of the diet (Galdikas 1988; Hamilton and Galdikas 1994; MacKinnon 1974; Rijksen 1978). Other foods include leaves, shoots, flowers, bark and insects. In Sumatra they have even been observed, on several occasions, eating slow loris (*Nycticebus coucang*; Utami and van Hooff 1997).

It is important to remember, however, that the relative proportions of the above food types in the diet can change dramatically over time, depending on what is available in the forest. As an example, Knott (1999) found that at times of the highest fruit availability fruit could comprise as much as 100 % of the diet in a given day. In contrast, she found that during periods of low fruit availability, fall-back foods such as leaves, pith, insects and bark comprised between 40 % and 70 % of the diet. Furthermore there seem to be some slight differences in overall diet composition between the two islands. Sumatran orangutans generally eating greater quantities of insects (e.g. ants, termites) than their Bornean relatives and lower amounts of bark (Ian Singleton, personal observation).

A particularly interesting finding of research in Kalimantan (Borneo) recently resulted from Cheryl Knott's research at Gunung Palung. The nutrient composition of 93 orangutan foods was analysed and combined with detailed data from 2441 feeding bouts to calculate total caloric nutrient intake (Knott 1999). Orangutans maximised caloric intake through consumption of carbohydrate-rich fruits during the high fruit period and maintained a positive energy balance, allowing them to build up fat reserves. During the low fruit period, orangutans reduced energy expenditure by travelling less but still

endured protracted negative energy balance. Ketones present in urine samples during the low fruit period indicated that orangutans were metabolizing fat reserves to make up for insufficient intake. As stated, this is of particular interest as it helps to explain why orangutans in captivity have such a high propensity for obesity. The forests of SE Asia are unusual in that they exhibit what is known as a 'masting' phenomenon. This describes periods when almost all fruit species in the forest fruit at the same time. The idea is considered to be a method of avoiding all seeds being eaten by seed predators (i.e. if all trees produce seeds at the same time and the population size of the seed predators is limited by the periods when only a few trees fruit, then there is no way that all seeds from even an individual tree are going to be eaten, thus guaranteeing that each tree has a good chance to reproduce). The orangutan is adapted to this highly cyclical (i.e. fluctuating) abundance and scarcity of fruit, and able to rapidly store fat reserves to cope with the periods of scarcity. This is in contrast to the other apes, as African forests do not exhibit such a marked seasonality (read periodicity) of fruit abundance and scarcity. They therefore do not need to be able to store fat quite as readily.

It would appear from the above that there is considerable scope for variation in captivity if we are to try and mimic a wild orangutans diet, both in quantities of the different food types available and also in the temporal provision of different foods (i.e. giving predominantly fruit in one month and reducing this amount, and instead providing more fibrous vegetable matter and even animal matter during other months). Radical changes to zoo diets should only be considered, however, with full consultation of captive animal nutritionists.

Social organisation

The orangutan is often referred to as an essentially solitary creature, with the exception of females travelling with their dependent offspring. However, again, information from Suag Balimbing has shed some new light on the subject. At Suaq, van Schaik (1999) found that females had a mean 'party size' of 1.67. This roughly equates to females spending about 67% of their time in association with other, non-dependent individuals. Based on his findings he proposed that female orangutans actually live in fission-fusion societies, that split and regroup to some extent, much like chimpanzees. Similarly, Wich et. al. (1999) published evidence from Ketambe that orangutan females may even be as social as chimpanzee females. Both findings therefore proffer a quite different perspective from the normal 'solitary' orangutan. Furthermore, there are a number of additional articles that refer to groupings or aggregations of orangutans at Ketambe (e.g. Rijksen 1978, Sugardjito *et. al.* 1987). However, at Ketambe, with a mean density of ca 5.0 individuals per km² and lowland hill forest these aggregations were predominantly in and around large strangling figs with abundant fruit. In contrast, the Suaq Balimbing animals often travel together, sometimes for several days. This was particularly noticeable for females with very young infants (< 1 year). In any case, it seems that when ecological conditions permit, orangutans do indeed tend to become more sociable.

The subadult, 'unflanged' male phenomenon

The physical development of non-flanged males into fully adult flanged males can be delayed for many years (See Orangutan Development, Reproduction and Birth

Management Chapter, this volume.) One case at the Ketambe study site in Sumatra documented a 33-year old male whose secondary sexual characteristics took 20 years to develop, presumably due to overlap of home ranges where the other animal was an older male (Utami and Mitrasetia 1994). Non-flanged males also do sire infants (Utami 2000). In captivity, the animals become sexually mature and capable of producing young between the ages of 6 and 10. Males do not begin to develop their most striking secondary sexual characteristics until up to seven years or more later. Males that have completed their first stage of development retain many of the physical characteristics of the adolescent such as short hair, hard rims on the side of the face and a flat chest. After remaining in the sub-adult or unflanged stage for a period of years, the male starts to develop the fatty cheek flanges and the large throat pouch of the mature or flanged male. The larynx also develops, the hair lengthens and thickens, there is general body growth and a musty scent becomes apparent. Once these characteristics begin to develop, the animal grows rapidly and full flange expression is often reached within a year (MacKinnon 1974). Kingsley (1982) documented that, in captivity, the development of these secondary sexual characteristics can be retarded when sub-adult males are housed in the presence of adult (flanged) males (See Orangutan Development, Reproduction and Birth Management Chapter, this volume).

Mating strategies

Generally, there are three categories of sexually active orangutans and each adopts a different mating strategy. These differences have been broadly summarised in Table 1.

Table 1.
Individual reproductive strategies of adult orangutans. Modified from van Hooff (1995); taken from Delgado and van Schaik (2000)

Adult Females:	Prefer to mate with males with the highest resource-holding potential, usually the locally dominant flanged male. Initiate consortships at times of high ovarian activity. Resist matings by unflanged males and subordinate flanged males unless there is little or no cost. When lactating, possibly keep track of familiar flanged males by their long calls for protection against infanticide, but to date there is little evidence to support this.
Unflanged Males:	Seek and attempt matings with adult females, despite restricted access due to high proportion of flanged males, infrequent encounters, and high costs of association. When females resist, force copulations. DO sire infants!
Flanged Males:	Given female preference for males with high resource-holding potential, attain locally dominant status and broadcast presence using long calls. Attempt to exclude all other males from

receptive females, and maximize length of consortships commensurate with the energetic costs of association. If not locally dominant, force copulations with females.

The relatively large size of each female's home range, coupled with the orangutans slow movement, limits the ability of males to defend their ranges and maintain exclusive access to females. Instead, there is emerging evidence that localised 'clusters' of females exist, whose members preferentially associate with each other and synchronise reproduction (Singleton and van Schaik 2002). Thus a dominant adult male seeks to control access to small clusters of females within his range, as and when the cluster members are receptive. Other males, on the other hand, appear to attempt to exploit irregularities in the synchronicity and search for females who may for whatever reason be receptive when the dominant male is not around (e.g. in the event of infant deaths, or newly maturing nulliparous females who are not yet synchronised).

Observations at Suaq Balimbing suggested that there were 'clusters' of females, whose ranges overlapped considerably, who were often very similar in appearance and who normally had infants of the same age. Examination of association patterns also showed that females within these clusters appeared to prefer each others company during associations to that of females from other clusters. These observations are therefore consistent with the idea that female offspring settle in ranges very close to and often overlapping that of their mother. What is perhaps more interesting is the reproductive synchrony within these clusters. It was noted at Suaq that there was only one clearly dominant adult male. He was observed to spend most of his time in any given year in the area where the resident female 'cluster' was ready to conceive. Furthermore, during the entire Suaq study, no other fully flanged adult males were seen to mate with any females. Instead, the only matings that didn't involve the dominant male involved unflanged subadult males and were usually forced. What seemed to occur is that when a cluster was receptive, the dominant adult male would tend to be around and in consort with females during their periods of oestrus. He and the females were also often accompanied by a variable number of unflanged males circling around the consort, presumably seeking an opportunity to mate whilst the dominant male was unable to intervene. In contrast, other fully flanged males tended to avoid these aggregations at such times. They were more commonly encountered in the study area when the dominant male was absent, and unflanged males were fewer, but more importantly during periods when females tended not to be receptive.

Inter-island differences

A number of distinct differences now seem evident between the behaviour and social organisation of orangutans on the two islands. To fully understand the captive behaviour of each species it is therefore useful to try and summarise these differences here.

INTER-ISLAND DIFFERENCES (Taken from Delgado and van Schaik 2000)

Densities of orangutans on Sumatra are approximately twice as high as in similar habitats on Borneo and the biomass of primates and other mammals is also higher on Sumatra. The orangutan's altitudinal range also appears to be much higher in Sumatra. Sumatran orangutans tend to spend more of their feeding time eating fruit and insects and less on the cambium growth layer of some trees. Together with the higher gregariousness of Sumatran orangutans, these differences suggest that Sumatran forests are more productive than Bornean forests. Although a thorough inter-island comparison of soil types and productivity is needed, the ecological factors underlying the differences may well be tied to divergent geologic histories that included extensive uplift and volcanism in Sumatra, producing much higher soil fertility. Higher soil fertility generally results in higher productivity and, consequently, a higher density of orangutans. Both habitat productivity and orangutan density, then, are likely to influence behavioral traits such as long call rates, rates of encounter, costs of association and therefore the reproductive tactics of both sexes. Future work should establish whether this contrast between the islands is true for all populations, and thus taxonomically based, or simply due to the nature of the sites sampled. In the latter case, areas should occur where the pattern associated with the other island is seen.

Adult male reproductive tactics vary between Bornean and Sumatran populations, particularly among subordinate flanged and unflanged males. Flanged males in Borneo engage in short consortships and use both forced and unforced copulations when mating with females, with the majority of forced copulations performed by either small or low-ranking males. Bornean flanged males are also more than ten times as likely (~24%) to force copulations than their Sumatran counterparts (2.3%), though still far less than unflanged males. In contrast, subordinate flanged males in Sumatra rarely achieve matings, but both the dominant flanged male and unflanged males can maintain long consortships with females. This difference may be a consequence of systematic differences in habitat quality between the Bornean and Sumatran sites. Bornean males, living in relatively poor habitats and more limited by energetic constraints than Sumatran males, are only able to sustain brief consortships. Low habitat quality also results in lower densities and less frequent rates of association. As a consequence, males probably have little or no knowledge about the females they encounter and are likely to be more aggressive in their mating attempts. In contrast, Sumatran males, living in richer habitats at higher densities, encounter females more often and are capable of maintaining longer consortships and sustained associations with females likely to be fecund.

Unflanged males on both islands actively seek and follow females and engage in consortships that often involve forced copulations. A striking difference, however, is that 90% of the matings between unflanged males and adult females in Borneo involve forced copulations whereas forcing characterizes only about 45% of the matings in Sumatra. On both islands, these males tend to be more constrained in the length of their consortships by social factors such as the presence of flanged males. In Sumatra, it is possible that the difference reflects a greater degree of monopolization of females in their fecund period by the resident dominant flanged male. This restricted access is more likely in habitats

with high productivity where preferred flanged males can maintain longer consortships, making forced matings less likely. An alternative explanation for the island difference would be that Sumatran females display a lower degree of resistance as a result of higher encounter frequencies or lower mating costs. Another remarkable difference concerns the relative proportion of flanged males. Although adult sex ratio is near parity across all sites in Borneo and Sumatra, in Borneo, on average, there are 1.6 times as many flanged males as there are unflanged males. In Sumatra, on the other hand, there are nearly twice as many unflanged males as there are flanged males. Perhaps, Sumatran males are more susceptible to socially induced delay in acquisition of secondary sexual characteristics, not inconsistent with the greater density of flanged males. Such a response could be adaptive in light of the greater monopolization of females by dominant flanged males in Sumatra, making the reproductive success of non-dominant flanged males close to zero.

Mating behaviour

Observations in the wild of consortship periods between fully flanged adult males and adult females of both orangutan species document a major involvement in the female initiating sexual behavior with these adult males. These consortships are usually initiated by the females which at the time of estrus seek out fully adult resident males with whom to copulate. Consortships can last between a few hours to several months, but most last 5-6 days (Rodman and Mitani 1986; Nadler 1988; Fox 2002). The location of the male is presumably known to the female on the basis of the long call, emitted by the male. The long call consists of a 'bubbly' introduction which builds up slowly into a climax of full roars, then trails off gradually into a series of 'bubbling' sighs (MacKinnon 1974). The purpose of the long call is generally considered to be a combination of advertising the male's presence to estrous females (Rodman 1973a, Rijksen 1978, Galdikas 1983) and/or as a spacing mechanism for potentially rival males (MacKinnon 1974, Mitani 1985). Among wild adult males the long call is also sometimes accompanied by a display, involving branch shaking and generally throwing his weight around whilst at other times he can be virtually motionless throughout, even sitting in a nest.

Captive mating behaviour

Both forced copulations and consortships have been documented in captivity (Nadler 1994). These strategies were not exclusive of each other within a given pair, but rather all pairs observed exhibited a mixture of both strategies (Maple 1980). In a captive setting, most copulations initiated by males involve chasing of the female. In contrast, female-initiated copulation attempts generally involve no chasing. When the length of copulation bouts with respect to the presence or absence of chasing was compared, copulations preceded by a chase were significantly longer than those which were not initiated by a chase (11.5 minutes compared to 2.3 minutes) (Maple 1980). The chase element is generally characterized as being aerial, involving several circuits of the animals' enclosure. This chase component does not appear particularly aggressive nor does it seem to induce fear in the female. Following a chase, the female submits or is wrestled down by the male and generally lies on her back on the floor or in an elevated location. The male then approaches her, inspects her genitals, and then mates

with her (often in a crouching or sitting position). Although the predominant position during copulation has been reported as ventro-ventral, many varied positions and postures have been observed, including dorso-ventral (with the female lying on her stomach or standing quadrupedally) or with both animals suspended, i.e., hanging from climbing structures. The duration of copulations is extremely variable, but can last up to 15 minutes (Maple 1980).

Although less often observed, female orangutans do exhibit proceptive behavior. The following proceptive behaviors have been observed in captive females: hand-genital contact, mouth-genital contact, rolling the male on his back, dorso-ventral and ventro-ventral mounting and pelvic thrusting (Maple *et. al.* 1979). This proceptive behavior appears to correlate with ovulation (Maple *et. al.* 1979; Nadler 1988; Fox 2002).

Since all aspects of orangutan behavior are directly related to adaptations to their wild environment, duplicating these conditions in captivity is challenging. For example, many captive orangutans have been and are maintained in larger social groupings than their wild counterparts appear to adopt, yet orangutans appear to be adaptable to changes in social structure under artificial living conditions. Traditionally, zoos have not duplicated natural social structures due to lack of enclosure space and presumably because the smaller solitary or small social units found in the wild do not offer as much exhibit potential as larger groupings of orangutans. As a result, many natural behaviors are often misunderstood or may be exhibited out of context in a captive setting (i.e. males forcibly copulating with females or adult males throwing and banging objects in their enclosures when they are long calling, both normal behaviours if compared to their wild counterparts). Therefore, knowledge of wild orangutan behavior is essential in helping to interpret captive interactions and can be useful in overall species management.

BEHAVIORAL ONTOGENY

Behavioral ontogeny has been examined in both wild (Horr 1977; Bard 1992) and captive orangutans (Maple *et. al.* 1978; Bond and Block 1982). The development of orangutans is characterized by a long period of dependence and, in the wild, a social unit comprised primarily of the infant's mother and possibly older dependent offspring. Horr (1977) describes the developmental process of wild orangutan as "growing up in a female world." Table 2 details the developmental stages of wild orangutans. Play behavior has also been studied in captive orangutans (Zucker *et. al.* 1986a).

Infant development

Recent work by van Noordwijk and van Schaik (in prep.) has summarised some of the observations on infant development in the Suaq Balimbing population. To quote directly "in this arboreal ape, 3 year olds had largely reached locomotor independence. Nest building skills were also well developed in 3 year olds, but immatures slept with their mother until weaned at around age 7. At the time of birth of a new sibling, association with the mother began to decline for both male and female offspring, suggesting that the immatures had mastered all the

necessary skills, including basic tool use, to feed themselves. By about 11 years of age, they also ranged independently from the mother.” The authors also agree with previous reports from Borneo (Galdikas and Wood 1990, Knott 2001) that the average interbirth interval in Sumatra is also around 8 years. Thus consecutive infants overlap only relatively briefly in their association with the mother, on both islands.

Taking on board the details above it is possible to construct a basic summary of the main developmental life stages of orangutans as follows in table 2:-

Table 2: Some important developmental life stages in wild orangutans (adapted from van Noordwijk and van Schaik [in prep.] and Rijksen 1978).

Age	Developmental status
3	Infants approach locomotor competence (although they still need help to cross major gaps), can build nests but still sleep in their mother's, and begin to spend some time in another tree, different to the one the mother is in. Prior to age 3 they are almost always within the same tree as the mother if not on her body itself, and almost always still carried by the mother during travel. These infants possess light pigmented zones around the eyes and muzzle which contrast with darker facial pigmentation; hair surrounding the face tends to be long and often standing out untidily. During their first year they are largely dependent on the mother for food but will begin to experiment with foods themselves after this. Three-year-olds also still invariably sleep in with the mother in her nest.
7	Offspring are weaned at this age and therefore become classified as 'juvenile'. Mothers stop playing with their offspring and become less tolerant of them around food (e.g. sending them away or refusing to grant access or share). The youngsters begin to sleep in their own night nest from this age onwards and proximity (i.e. the amount of time the offspring spends within 10 m of the mother) begins to decline dramatically. By age 7 the offspring has already achieved an adult-like activity budget and foraging competence such that they can both find and process food items themselves. They will also try to play with peers whenever they have an opportunity to do so. At this age the pink rings around the eyes are normally still clearly visible, at least on the eyelids, but the face and muzzle is beginning to darken.
8	Around the time the next infant is born the youngster begins to spend much less time within 50 metres of its mother and can spend several days away before returning for a few days.
10/11	The offspring has now reached adult levels of association (i.e. spends around the same amount of time near its mother as any other, unrelated, adult orangutan in the neighbourhood). Thus they have reached ranging competence, meaning that they are both able to travel significant distances and navigate effectively on their own. This stage is the

beginning of what would normally be termed adolescence. Initially facial colouration still has the obvious light patches, but gradually begins to change from now on to completely dark. Still shedding deciduous teeth and may continue to do so until around 13 or 14 years of age. Males and females can be difficult to distinguish unless there is full view of anogenital region as they can be very similar in facial characteristics and in size and weight. Males, however, gradually become heavier (adding bulk and muscle) and females begin to take on the form of leaner, lighter versions of adults. More and more they begin to seek contact with peers, often travelling in pairs or small groups. They also tend to be cautious during contacts with adults, especially adult males, but their curiosity increases as they begin to explore their own sexuality.

- 15 This is the average age at which females give birth to their first infant and can hence be regarded as truly adult. Males on the other hand may well be capable of siring infants before this age but may not actually manage to do so until they are older. The age at which wild male orangutans sire their first infants is not adequately known but in captivity they are generally potent some years before now, as are females. Males come to be regarded as 'subadult' or 'unflanged' in their early teens, if they haven't already progressed to fully flanged adulthood. By now they will have developed a fuller beard and can begin to exhibit hard rims of undeveloped cheek flanges on the sides of the face. In many cases this is accompanied by the hair surrounding the face appearing shorter and more flattened against the skull. Testicles are easily visible with binoculars. Subadult males weigh approximately 35 kg to 60 kg. Both male's and female's faces become completely dark (with some exceptions that retain pink eyelids well into adulthood). Some females may develop a beard and a small throat sac, and can hence still be difficult to distinguish from subadult males without a clear view of the genital area, unless accompanied by an infant. As mature adults females generally weigh between 40 and 55 kg. Fully flanged adult males are extremely large animals reaching in excess of 100 kg. They also exhibit maximal development of secondary sexual characteristics including cheek flanges, a full beard, large throat sacs and much longer, shaggier hair than subadult males and adult females. They are both sexually and socially mature and generally travel alone (unless in consort). They also emit the characteristic long-distance vocalisation known as the "long call".

BEHAVIORAL REPERTOIRE

The range and complexity of orangutan behavior, vocalization and facial expressions are too extensive to describe in written format here. A complete ethogram cataloging wild orangutan behavior can be found in MacKinnon (1974) and for captive behavior in Maple *et. al.* (1978). See Maple (1980) for a compilation of orangutan ethograms. Table 3 presents a list of behaviours noted among captive orangutans while similarly, Table 4 provides an ethogram developed by Rijksen (1978), listing behaviours observed among wild orangutans, at the Ketambe study site in Sumatra.

Table 3. Behaviors of captive orangutans (adapted from Maple *et. al.* 1978)

<u>Behavior</u>	<u>Description</u>
Cradling	cradling infant on the floor or in arms.
Holding infant	holding infant either on the floor or in the air.
Pushing	pushing or sliding infant ventrally or dorsally on the floor.
Ventral riding	infant carried on mother's ventrum.
Dorsal riding	infant carried on mother's back.
Clinging	infant clinging to mother.
Nursing	infant suckling from nipple unaided.
Facilitate nursing	mother moving the infant to the nipple.
Deter nursing	mother moving the infant away from the nipple.
Retrieve	retrieve infant from another animal or physical structure.
Present infant	present infant to another animal.
Break contact	contact broken between mother and infant, but proximity maintained.
Standing while grasping	infant standing while grasping mother.
Standing alone	infant standing alone.
Locomote with contact	infant locomoting (crawling, walking) while in contact with mother.
Locomote alone	infant locomoting (crawling, walking) independent of mother.
Digit sucking	sucking one's own fingers or toes, or those of another animal.
Inducing manipulation	mother placing infant's hand, etc., in contact with any object.
Hanging alone	infant hanging from bars by him/herself.
Proximity	a distance of one body width or less from another animal.
Withdraw	move out of proximity.
Touch	contact of one object or body part to another object or body part.
Groom other	one individual picking, stroking or parting of hair over any part of the body with mouth or hands of another individual.
Groom self	picking, stroking or parting of own hair over any part of the body.
Hand extension	extending hand towards another animal.
Hand-hand contact	mother holding or touching hand of infant.
Mouth-mouth Contact	mouth, lips or tongue in contact with another individuals mouth, lips or tongue.
Hand-genital contact	one individual touching hand to another's genital area.
Mouth-genital contact	one individual touching mouth, lips or tongue to genital area.

Olfactory inspection	sniffing one's own hand after contact with another animal, or putting nose to another's body.
Sleeping	resting without locomotion eyes are closed.
Brachiate	hand-over-hand locomotion.
Walk quadrupedally	forward or backward locomotion involving hands and feet simultaneously.
Walk bipedally	forward or backward locomotion involving both feet. Arms are usually held over the head.
Mount	mounting another animal in a copulatory position; genital-genital contact established.
Sexual present	presenting ano-genital region to another animal.
Ventro-ventral copulation	copulation with animals in full ventro-ventral position.
Dorso-ventral copulation	copulation with one animal mounting the other in a dorso-ventral position.
Yawn	opening of mouth and lips with teeth bared or not visible.
Baring teeth	open mouth with teeth visibly directed towards another animal.
Grimace	teeth showing, mouth slightly open, corners pulled back.
Kiss squeak	vocalization made by the intake of air through extended lips (MacKinnon 1974).
Long call	deep, rumbling vocalization (MacKinnon 1974).
Grunt	deep, belch like vocalization (MacKinnon 1974).
Funnel face	maximal pursing of the lips.
Chase other	individual pursuing another using any form of locomotion.
Displace other	assuming the physical location that another animal had occupied.
Bite other	bearing down on body part of another individual using mouth or teeth.
Hit/grab	contact with another animal with either an open hand or fist.
Wrestle	wrestle with or roll with another animal.
Mouth fighting	reciprocal, non-aggressive biting.
Self-feeding	lacing an edible item in own mouth.
Take food	take food from another animal's mouth or hand.
Give food	give food to another animal.

Table 4. Ethogram developed from observations of wild orangutans in Ketambe, Sumatra, (Rijksen 1978).

advance	hesitate approach
approach	hesitate avoid
arm wave	hide
avoid	hitting
bared-teeth scream	hit away
bark	hold out hand
bark-biting	horizontal bared-teeth face
biting	ignore
branch waving	kiss sound
breaking/dropping of branches	leave
bridging	long call
brusque charge	look at mouth
bulging lips	lork call
chomping	loutish approach
circling	masturbate
clinging; tandem walking/climbing	mating squeals
contact cuff	mounting
copulation	mouth-mouth contact
diving	muzzle-pushing
dragging, pulling	nest-building
ducking	open-mouth bared teeth face
embrace	ostentatious approach
fixed gaze (stare)	penile erection
fleeing	positioning
flinch	posturing
follow	pout-moan
frowning	presenting
gathering	rest
genital inspection	rocking
gnaw wrestling	scratching
gnaw wrestling with relaxed open mouth face	scream
grasp	self-decorate
grinding	self-grooming
grooming	stiff approach
grumbling	struggle
grumph	temper tantrum
grunt	tense-mouth face
gymnastics	throat-pouch inflation
hand-wrestling	throwing
hesitate advance	touch and smell

GROUP SIZE AND COMPOSITION IN THE WILD

The most commonly encountered 'grouping' of wild orangutans is solitary individuals or mother-infant dyads (sometimes with the youngest and the older offspring at the same time). However, on occasions, more than one adult female and infant(s) may be found feeding or travelling together and subadult, unflanged, males will also sometimes travel in small groups of two or three as they scour the area. These groupings are not permanent social groups like those found in other diurnal anthropoids but for sure there is some tendency toward sociality among some age/sex classes and at some times, even if more often in Sumatra, and in contrast to what is often the perceived norm for this species. Aggregates of this type can occur in particularly abundant food source, such as a large fruiting fig tree. Rijksen (1978) observed group associations, i.e., associations of individuals other than mothers with dependent offspring, in the Ketambe study site in Sumatra. These associations consisted of individuals within visual range of one another showing coordinated movements (17% of observed groupings), and temporary associations consisting of individuals feeding in the same tree but separating after completing their foraging bout (37% of observed groupings). Similar observations regarding social groupings have been noted by Galdikas (1984) and MacKinnon (1974). However, research at Suaq Balimbing shows that 'parties' (i.e. associations between two or more independent orangutans) can be far more common than was previously realised (see van Schaik 1999, Singleton and van Schaik 2002). On the one hand adult females frequently travel in loose groups (which can be spread over as much as 50 metres or more but without doubt involving individuals that are following one another. Subadult unflanged males will also often travel with their peers for some time, even weeks or months, as they search for unguarded females to harass. Presumably, the ability of orangutans to socialise will depend largely on the ecological constraints imposed by the environment in which they live. If in a particular habitat type a female would have to journey twice as far in a given day to find enough food as a result of travelling with a peer she is unlikely to do so. If however, the abundance of food permits her to travel with a peer, and still traverse a similar distance per day as she would if feeding alone, then socialising becomes more possible and hence likely. In his 1999 paper, van Schaik even went so far as to suggest that female orangutans at Suaq Balimbing live in fission fusion societies, much as female chimpanzees do.

The implication is that where the habitat allows, i.e. where orangutans are able to live at higher densities, they do indeed start to become more sociable. Where ecological constraints mean densities must be much lower, it may be true to say that orangutans still strive towards this goal but are prevented from being sociable as they simply don't have the time or can't expend the energy that would be required if they were to seek company more often. An explanation along these lines would go a long way towards explaining the orangutan's undoubted propensity and willingness to socialise in captivity, at least among a large proportion of individuals. Exploring the "social potential" of orangutans, Edwards (1982), already suggested this when writing that environmental conditions in the wild preclude high levels of sociality but that orangutans have the potential for plasticity in social behavior that is expressed under captive conditions.

RELATIONSHIPS BETWEEN INDIVIDUALS IN CAPTIVITY

In the wild, offspring remain with their mothers at least until the birth of the next infant (i.e. ca 8 years). Before this time the youngster will have already begun leaving its mother for short periods but after this time, such absences gradually become both more frequent and longer. Nevertheless they will continue to 'visit' their mother for some years. Females appear to settle near their mothers, in adjacent and overlapping ranges whilst males disperse farther (Galdikas 1995, Rodman and Mitani 1986, Leighton and Leighton 1983). Interestingly, this is unlike the pattern observed in the African apes where the females tend to be the dispersers. The adult male plays no role in parental care of his offspring (Horr 1977).

In captivity, juvenile orangutans are typically removed from their natal group when aggression between adults and offspring is observed or there is a risk of inbreeding. Maple (1980) reports a consensus among zoo personnel that aggression may occur when juvenile animals attempt to interfere with copulatory attempts between an adult male and the juvenile's mother. However, even very young infants and juveniles may do this, and normally without any repercussions. It is therefore more likely that it is not simply the 'interference' that precipitates the aggression but more the size and status of the maturing juvenile. It is important to note that juveniles are often removed from the natal group for reasons other than adult-juvenile aggression. Recommended moves by the Species Survival Plan (SSP)©, normally for breeding purposes, and space constraints are just two of many reasons why an individual may be removed from its natal group.

In Maple *et. al.*'s 1979 study of captive mother-infant pairs, researchers documented the occurrence of "maternal mounting" of infants as well as oral and manual manipulation of the infant's genitals. Their data suggests that this behavior may be beneficial to the normal development of sexual behavior in young orangutans.

Adult male and offspring

While virtually absent from an infant's social environment in the wild, adult males in captivity are often housed with females and their offspring. Adult males appear to be adaptable to a variety of social settings in captivity, and they have been known to show extreme tolerance and interest in infants as well as in juvenile conspecifics (Zucker *et. al.* 1986b). In one instance, when a female was separated from her 23-month-old male offspring, the 28-year-old sire even took over the care of the infant. This male actively solicited the infant to ride on him when moving between exhibits. The infant was routinely observed suckling on the adult male's cheek pads and later on his nipples. This behavior was observed over a 25-month period (Carol Sodaro, personal communication). This is not an isolated instance (Lori Perkins, personal communication). Captive males have also been observed to actively engage infants and juveniles in play behavior and food-sharing behavior (Zucker 1994). Since both individual orangutans and the

environments in which they are kept in vary markedly, any decisions regarding leaving an adult male in with a pregnant female or female with young offspring should be evaluated on a case-by-case basis (Development, Reproduction and Birth Management Chapter, this volume).

Adults of the same sex

As noted, in the wild adult and subadult males play virtually no role in the care of infants that they sire. In similar fashion they do not interact to any large degree with adult females and younger animals, unless in consort (or in the case of subadult males, attempting to force copulations). However, in captivity both morphs of males are routinely housed with other orangutans of all ages, including adult females and their infants. Despite this, aggression between males and females in captivity is relatively uncommon (though of course not unheard of).

In contrast, aggression between members of the same sex seems distinctly more common (Ian Singleton, personal communication). Most zoos with more than one or two subadult or fully adult males have experienced difficulties in housing them together, often with the result that they must be housed separately all of the time. Likewise, personal experience also shows that females are highly variable in the degree to which they will tolerate being housed with other mature females. This can be clearly evident either as blatant aggression, in which one attacks another, or more subtly, and only noticeable through careful observation (such as one individual consistently moving away when the other approaches or enters the same area).

When introducing individuals to each other and in their general management the importance of observing the animals cannot be understated. On the one hand, if something goes wrong it is essential to try to understand why and if possible which orangutan was responsible. Without watching what happens we learn nothing from these events and are liable to make the same mistakes again and again. Furthermore, orangutans do not generally display the same range of vocalisations and facial expressions (or at least do so in a more subtle way) as do the other apes. We therefore have to observe closely in some situations before we get even the faintest understanding of what is really going on between individuals, even in situations that at first glance might seem perfectly harmonious.

A NOTE ON 'ABNORMAL' BEHAVIOR

Abnormal behavior is generally regarded as that which may occur in captive animals that is substantially different from the behavior of their wild counterparts, either in degree or kind. Typically, such behaviors are construed as undesirable. However, high levels and increased sociality are all patterns of captive orangutan behavior that until relatively recently had not yet documented in the wild (Maple 1980). They have at times therefore been regarded as abnormal. The results of studies in Sumatra, however, support the contention that in an environment that allows increased sociality, even wild orangutans will be consistently more social. We therefore suggest that optimum

conditions for orangutans probably do allow the opportunity to socialise and hence that habitats that do not are perhaps sub optimal for this species. Unfortunately though, sub-optimal habitat is rapidly becoming all that is left for wild orangutans!

Abnormal behaviors occurring in some captive orangutans include lack of maternal skills, stereotypic behaviors, atypical sexual behavior and hyper-aggressiveness. Changes in social groupings, improved housing, behavioral enrichment and positive reinforcement training are known to alleviate some of these undesirable behaviors.

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