

# Development of independence

## Sumatran and Bornean orangutans compared

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### 12.1 Introduction

Compared with other mammals and even other apes, orangutans have a very long interbirth interval of 6–9 years (see Chapter 5). Given the tight association between mother and infant, this implies that mother orangutans invest more time than other apes in each offspring. Therefore, one would assume that, compared with its close relatives with shorter interbirth intervals, orangutan immatures require more time to grow to a size and/or acquire the skills required to survive and

thrive without their mothers' undivided care. Yet orangutans do not seem to differ significantly from their closest relatives in the time needed for growth (at least in females: Leigh [1996]), or in the quantity or complexity of skills that need to be learned before reproduction. In fact, recent studies of two different natural populations of Sumatran orangutans (van Noordwijk and van Schaik 2005; van Adrichem *et al.* 2006) concluded that these orangutans acquire competence in skills, such as locomotion, food processing, nest building etc., at about the same age as reported for wild chimpanzees

(Pusey 1983, 1990; Hiraiwa-Hasegawa 1989; Watts and Pusey 1993). In addition, chimpanzees and Sumatran orangutans start to range independently, i.e. give up the permanent association with the mother, at about the same age, suggesting they reach the size and level of skill to do so at about the same age (Pusey 1983, 1990; van Noordwijk and van Schaik 2005; van Adrichem *et al.* 2006).

Recent reviews of the slow life history of great apes focus on the causes and implications of their generally long pre-reproductive period (van Schaik *et al.* 2006b). However, current hypotheses cannot explain why the orangutan's interbirth intervals would be so much longer than those of other apes. Van Noordwijk and van Schaik (2005) suggested that the orangutan's ecologically imposed solitary lifestyle, preventing even independent immature offspring from associating with their mother, was largely responsible for the relatively prolonged interbirth interval of Sumatran orangutans. Thus, whereas chimpanzee mothers tend to range in the company of multiple offspring (a phenomenon we have called 'offspring stacking'), Sumatran orangutans rarely do so. Since their developmental timescale seems to be very similar, however, this difference implies that orangutans will master essential skills before weaning to a larger extent than chimpanzees, who are weaned at a relatively earlier phase of their skill competence level.

The solitary lifestyle hypothesis may be insufficient to explain the life history of all orangutans: Bornean orangutan populations are reported to differ from Sumatran ones in several parameters, such as having a lower population density (see Chapter 6) and lower frequency of association between independently ranging individuals (van Schaik *et al.* 1999 and Chapter 17 this volume). These contrasts suggest lower habitat productivity for the Bornean populations studied to date, an expectation confirmed by detailed phenological comparisons (see Chapter 7). It would therefore be reasonable to expect that interbirth intervals of Bornean orangutans would be even longer than the 8–9 years reported for Sumatra (Wich *et al.* 2004b). However, the available data suggest the opposite: estimated interbirth intervals for several populations of Bornean subspecies seem to be around 6–7.5 years (see Chapter 5). This implies that Bornean

orangutans either develop faster to independence or stay in association with their mother after the birth of a sibling for longer than Sumatran ones, thus going against the prediction of the solitary lifestyle hypothesis. Either way, these differences may affect their survival.

To address this conundrum, we undertook to compile and compare data on orangutan development from both Sumatran and Bornean sites. Recognizing that mothers provide transportation, food, protection and social company, and function as role models for the acquisition of physical and ecological (foraging and ranging) skills, we explore the development to independence in all these domains for young Sumatran and Bornean orangutans in natural populations. In this chapter we compare the available information on the development of competence in transportation, nutrition, protection against the elements, social relationships, association and ranging for wild orangutans in two Sumatran (Ketambe and Suaq Balimbing) and three Bornean (Tuanan, Kinabatangan and Sabangau) sites.

Before examining the data, we must point out that the available developmental data on orangutans have various limitations. First, because of young orangutans' long dependence on the mother, and their late age of first reproduction (see Chapter 5), studies should ideally last decades. Only truly longitudinal studies can document the fates of known-aged immatures from birth to independence and the subsequent transition to reproduction. There is only one site for which such data exist: Ketambe. Elsewhere, studies are largely cross-sectional, and ages are accurately known only for younger immatures born during or shortly before the start of the study, whereas for the older individuals ages have to be estimated based on prior experience of the researchers. Second, in all field studies the behavior of many immatures could only be sampled at variable and sometimes rather long intervals, and it was not possible to follow independent immatures continuously. Therefore, the age at which an individual was observed to do something for the first (or last) time was always over- (or under) estimated with an unknown degree of accuracy.

The third limitation is that of sample size. Due to demographics the number of same-aged

individuals that can be observed at a given site is always small. Obviously, data on multiple mother–offspring dyads with accurately known ages are required to detect differences in development and its pace due to sex, maternal style and other factors. Samples sizes were too small in the two Sumatran studies (van Noordwijk and van Schaik 2005; van Adrichem *et al.* 2006) to detect sex differences in development and sample sizes are equally inadequate for the Bornean populations presented here. Here, we can only hope to provide a general impression of consistent variation, since rigorous statistical testing of intra- and inter-site variation is not yet possible. We hope that more complete data will become available in the future to document the road to independence of female and male orangutans in different populations in more detail to support or refute our preliminary findings presented here.

Data presented in this chapter were collected by different teams of researchers in the various sites. Still, all studies basically used the same methods of (nest to nest) focal animal sampling (for details see van Schaik [1999] and <http://www.aim.uzh.ch/orangutanetwork.html>). Table 12.1 shows the number of mother–offspring pairs and the total observation time per site.

In this chapter we refer to immatures as independent, when they are fully weaned and no longer in permanent association with their mother; and semi-dependent if they are newly weaned but still in permanent association with their mother. In Tuanan and Sabangau data were also collected on independent immatures estimated to be 5–9-years old at first encounter, who were never seen in association with a likely mother.

## 12.2 Dependence on mother for transportation

### 12.2.1 Carrying

During the first months of its life an orangutan is in almost constant body contact with its mother during all her activities. The total percentage of time in contact declines to less than 50% around the second birthday (van Noordwijk and van Schaik 2005; van Adrichem *et al.* 2006). However,

to measure the importance of the mother for transportation, we consider the percentage of time the mother is carrying her offspring while she moves through the canopy: when she travels, the mother almost always carries her offspring for the first two years of its life, and this gradually declines to less than 50% of time only over the next two years. Quantitative data on young immatures from Suaq, Ketambe and Tuanan, as well as the qualitative data from Kinabatangan, show that this pattern is remarkably consistent across sites (see Fig. 12.1). Although there is no evidence for a difference in skill level, the data seem to suggest that immatures sampled in the Bornean populations may be carried a little more when they are 2–4 years old.

This difference could be linked to the more uneven canopy structure in the heavily logged forests in which the Bornean orangutans were observed. On the other hand, it seems infants in Sumatra may occasionally be carried when over 6 years old, by which time they are never carried anymore in Borneo. This comparison suggests a very similar age trajectory in locomotor development, with perhaps a slightly later complete independence in Sumatra.

### 12.2.2 Proximity

Even after the mother has stopped regularly carrying her offspring, she frequently assists its travel from tree to tree by making a ‘bridge’ so that the smaller individual can cross a gap between trees.<sup>1</sup> Bridging is most obvious when a mother holds on to branches of the trees on either side of the gap until her offspring has clambered across, but she may also assist her child by swaying a tree closer to another and not releasing this position until the offspring has crossed. As long as the immature frequently uses its mother’s assistance in this way, it seldom ventures far away from her. As shown in Fig. 12.2 an immature spends more than 50% of its time within 10 m of its mother until it is at least 6 years old in Suaq, Ketambe and Tuanan. Six years

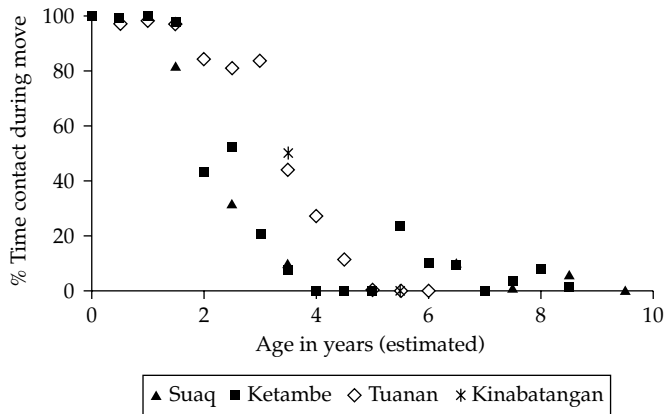
<sup>1</sup> In almost all case an immature over c. 4 years old will be able to get out of any tree without the mother’s assistance, but this may entail a detour either horizontally or vertically, thus making travel (and staying in close association with the mother) more costly.

**Table 12.1** Overview of data available per research site

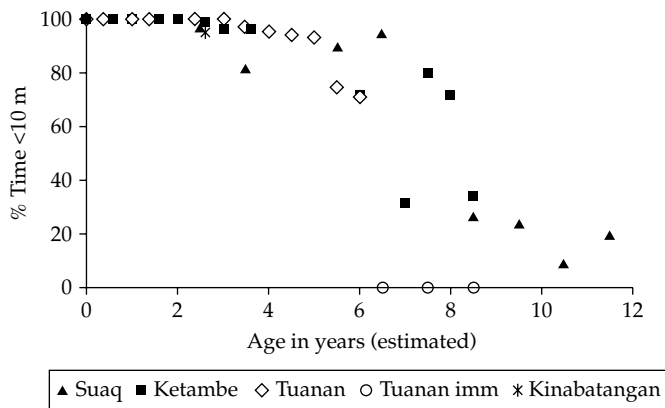
Site	Observation period	Focal hours		Age range in year <sup>a</sup>	No. of immatures <sup>b</sup>	Reference/data coordinator
		mothers	Dependent immatures	Independent immatures		
Sumatra						
Suaq	Feb 1994–Sep 1999	8835	155	2484	15	van Noordwijk and van Schaik 2005
Ketambe	Apr 1993–Oct 1995 Feb 1999–Aug 1999	1550		0–11+	4	van Adrichem <i>et al.</i> 2006
Ketambe	Aug 2003–Oct 2004 *	1951	1951	122	7	Sumatran Orangutan Conservation Programme–Nuzuar
Borneo						
Tuanan	Jul 2003–Aug 2005 *	5850	5850	320	7 (+3)	Tuanan orangutan project Universitas Nasional Jakarta– University of Zürich, Switzerland
Sabangau	2003–2005 *	1520	0	1258	2 (+4)	H. Morrogh Bernard
Kinabatangan	1999–2005 *	3804	0	0	1	A. Abulani and M. Ancrenaz

\* Ongoing focal observations on immatures.

<sup>a</sup>Numbers between brackets indicate estimated ages.<sup>b</sup>Numbers between brackets indicate immatures without known mother.



**Figure 12.1** The percentage of time offspring of different ages is clinging to their mother's body while she travels through the canopy for 4 different populations. Six-months averages are given per age class and site; individuals may contribute to several age classes over time. For Suaq, Ketambe and Tuanan averages are based on focal samples. For Kinabatangan 50% and 0% are based on qualitative data. Solid symbols are used for Sumatran populations, open symbols for Bornean populations.



**Figure 12.2** The average percentage of time offspring is within 10 m of the mother for immatures per 6 months age class in 4 different populations. For Suaq, Ketambe and Tuanan averages are based on half hour scores during focal follows of the mothers and/or the offspring. Note: Tuanan imm: independent immatures without known mother.

is also the age, according to qualitative data, after which bridging is hardly ever seen in Suaq, Tuanan and Kinabatangan.

Additional quantitative data collected in Tuanan (swamp forest with mostly small trees), indicates that offspring until *c.* 6 years of age spend more than 50 % of their time in the same tree as their mother. Qualitative data from Kinabatangan suggests the same. In Ketambe (primary dryland forest with mostly large trees), immatures spend most of their time in the same tree as their mother until they are at least 8 years old. Thus, immatures, even when they are no longer carried at all, spend much time close to their mother, and this may well be due to their dependence on her assistance in crossing gaps. This comparison of the development of locomotor independence therefore also suggests a slightly slower development to complete independ-

ence among Sumatran orangutans, but this difference could be due to differences in habitat rather than taxonomic position.

## 12.3 Mother as food provider

### 12.3.1 Nursing

Due to the orangutan's arboreal habits, it has proven to be virtually impossible to obtain a good estimate of the amount of time infants drink their mother's milk. Mothers may nurse their offspring inconspicuously while feeding and resting. When mothers rest on a nest they may also frequently nurse, but this remains hidden to any terrestrial observer. Thus, the collection of quantitative data on frequency and duration of nursing to document changes over time is not feasible under natural

conditions. However, the *end* of nursing (weaning) can be inferred to within a few months.

In most mother–offspring pairs the frequency and duration of nursing seems to decrease very gradually and in most dyads ‘weaning conflict’ interactions are observed infrequently. However, occasional nursing is observed for offspring up to at least 6–7.5 years in both Suaq (van Noordwijk and van Schaik 2005) and Ketambe (van Adrichem *et al.* 2006; and recent data 2003–2004). In contrast, in the Bornean sites, nursing was no longer seen when the offspring was 5–6 years old in one mother–offspring pair at Kinabatangan and when it was an estimated 5.5 years old in one pair at Tuanan. Although the small sample size hardly allows us to conclude that immatures are weaned at an earlier age in Bornean than in Sumatran orangutans, earlier weaning in Borneo would concur with the shorter interbirth intervals reported there.

### 12.3.2 Scrounging of solid food

Infant orangutans are allowed to take their first solid food from their mother’s mouth and mothers often actively make food available for a young infant to take. An infant over c.1 year old often begs by holding its hand to its mother’s mouth or directly tries to take food from her hands. Both mouth-to-mouth and hand-to-hand (or mouth-to-hand) transfers of food are frequent during an offspring’s first few years of life. Although both forms of food transfer are seen occasionally between unrelated independent individuals, including adults (van Noordwijk and van Schaik *in review*), the frequency and the number of different kinds of food the offspring begs and obtains from its mother steadily declines with age (Jaeggi *et al.* 2008).

From around the time of weaning onwards, mothers become less tolerant and generous toward their offspring’s scrounging and seem to tolerate only the taking of food items that are difficult to process or to recognize, such as pieces of rotten wood infested with termites: at c.5–6 years in Tuanan (Jaeggi *et al.* 2008), and around 7–8 years in Suaq (unpublished data). In Suaq, a mother allowed her 8–9-year-old independent offspring, but not an onlooking unflanged male, to take some of the

carcass of a slow loris she caught. Thus, mostly anecdotal data suggests an earlier onset of maternal intolerance in the Bornean than in the Sumatran populations, but more systematic data should be collected.

## 12.4 Mother as role model for the acquisition of skills

### 12.4.1 Feeding techniques

Riding on their mothers, orangutan infants carefully watch their mother’s feeding activities from an early age on. Once they are mostly moving by themselves, they can still often be seen paying close attention to what the mother is eating and how she is eating it. Furthermore the more difficult the food is to process, the more attention immatures pay when their mothers feed on it (Jaeggi *et al.* *in prep*). It is no surprise, then, that 3–5-year-olds in Tuanan were able to process everything their mothers ate (Dunkel 2006), and actually did process by themselves almost all food eaten (Massen 2004). However, as measured in Tuanan, immatures achieved lower feeding rates and thus lower efficiency in harvesting fruit than their mothers did in the same tree (Massen 2004; Dunkel 2006). Only the largest independent immature, almost the size of an adult female, was about as efficient as the adults.

Similarly, in Suaq, older (semi-)dependent immatures were able to process those foods for which tools were habitually used in that population (van Noordwijk and van Schaik 2005). Thus, in both Suaq and Tuanan, immatures had acquired, through social and individual learning, the necessary skills to process their mother’s diet before they were completely weaned. Unfortunately, detailed data on skill acquisition in the Sumatran populations are still lacking, so it remains to be determined whether all necessary feeding skills are acquired at a similar absolute chronological age or a similar age relative to the moment of weaning.

In sum, weanling orangutans from both Borneo and Sumatra have the skills to eat the same diet as their mothers, with the possible exception of very rare food sources.

### 12.4.2 Nest building

Until around weaning, irrespective of its actual age, an immature orangutan joins its mother in her nest for the night and daytime rest (see below). In all study sites, immatures are often attentive while their mothers build a nest and even seem to help with adding some branches, twigs or leaves. One–two-year-olds can be seen to ‘practice’ nest building while their mother is stationary, either feeding or resting. Observations in Suaq, Ketambe, Tuanan and Kinabatangan indicate that most 3-year-olds (and some younger ones) are well able to build adequate nests for a brief rest. Thus, immature orangutans, be they Bornean or Sumatran, have acquired sufficient nest-building skills long before they start to spend the night in their own nest.

### 12.4.3 Other physical skills

In addition to nests, orangutans may make other constructions, such as head covers and nest covers. In Suaq, Tuanan and Kinabatangan even very small dependent offspring (1–2 years old) were observed to make ‘rain hats’, independently of their mothers. Although their first exposure to these constructions is undoubtedly through their mothers, even orangutans growing up in captivity without their mother put things on their heads and thus they seem to have a strong disposition to cover their heads. In the wild, the skills to make appropriate hats as well as recognition of the suitable circumstances (rain) are acquired long before weaning in all populations for which data are available. It is worth noting, that for infants up to 3–5 years old there is no real thermoregulatory necessity for rain hats since most of the time they can, and actually do, cling to their mothers during rain. Again, immatures have mastered the skills long before they actually need them.

## 12.5 Mother as protector against the elements

### 12.5.1 Nest sharing

Even though immatures over 3 years of age are able to build their own nest, they tend to spend the night with their mother until they are 6–8 years

old in Suaq (van Noordwijk and van Schaik 2005), and Ketambe (data 2003–2004), and until they are c.5 years old in both Tuanan and Kinabatangan. Since nursing is nearly inevitable when mother and offspring share a nest, it is not surprising that the age at which offspring start to sleep in their own night nest corresponds with the age of weaning. Although data are still very limited, the observed difference between Sumatran and Bornean populations concurs with the inferred earlier weaning on Borneo.

### 12.5.2 Predators

Adult orangutans seem largely immune for predation as long as they stay in the trees. Apart from the tiger, which is assumed to prevent Sumatran orangutans from moving on the ground, clouded leopards and pythons are likely to pose threats to immatures throughout the orangutan’s range (Rijksen 1978). In Tuanan, a pilot study on the response to a model predator showed that mothers always detected both the model and its ‘neutral’ control earlier than their 2–5.5-year-old offspring (Nieuwenhuis 2006 and personal communication). After detection of the predator model, all these immatures made body contact with their mothers. Thus, at least until immatures are 5.5 years of age, mothers serve as detectors and protectors against potential predators. Similar experiments in other populations and over a range of immature ages would show whether this protection role of orangutan mothers is a general one.

## 12.6 Mother as social partner

### 12.6.1 Play

For many young orangutans, opportunities for social play are few and far between. Only their mother is permanently available as play partner, but even the most playful mothers do not seem to play with their offspring every day. In Tuanan, immatures of all ages spent on average less than one percent of their waking time in social play. However, when mother and offspring were in association with another mother–offspring pair, the immatures could spend up to 50% of their time

in social play with each other. Such opportunities were rare, however (mothers with unweaned offspring spent <1% of day time together). Of all social play time of dependent immatures about half was spent with other dependent immatures, a third with their own mother and the remainder with a visiting nulliparous female. The immature whose mother was starting to receive sexual attention from unflanged males sometimes had brief play interactions with such males. A similar pattern was observed in Kinabatangan.

One might expect more opportunities for play and thus more time spent playing in those populations with higher association tendencies. Unfortunately, no quantitative behavioral data on unweaned immatures are available yet for Suaq, which has the largest average party size of all studied populations (see Chapter 17). In the other Sumatran site, Ketambe (with intermediate average party size), unweaned immatures less than 6 years old spent an average of 1.5 % of their time in social play (based on 1356 hours of focal sample). Weaned immatures in both Suaq and Ketambe spent on average only 0.5–1% in social play. No mother at either site was seen to play with her offspring once it was over 7 years old and weaned, even those who had regularly played with their infant before and during the last phase of weaning. Thus, even in the most gregarious populations, immatures actually spend very little of their time in social play, even though they seem to take advantage of all available play opportunities.

In contrast to social play, young immatures spend a considerable part of their time playing by themselves. Thus, solitary play with objects (twigs, leaves, fruits, lianas) or repetitive locomotor play (including swinging, swaying, twirling either upside down or head-up) can take 15–45 % of their active time (Suaq, Ketambe and Tuanan: no indication of inter-site differences). By the time they are weaned, however, immatures hardly engage in solitary play anymore (<2 %) in any site.

### 12.6.2 Grooming

Unlike, all other anthropoids, orangutans spend hardly any time at all on social grooming (<0.01%), much less than chimpanzees (5–10% of time):

(Wrangham 1977; Ghiglieri 1984; Pusey 1990). Mothers groom their young offspring, but do so too infrequently to give a reliable estimate of any trend with offspring age. Even though some allogrooming may happen on the nest, outside the view of terrestrial observers, it is unlikely that any significant amount of time is devoted to this in any orangutan population.

Despite relatively frequent associations and a high level of social tolerance in the Suaq population allogrooming outside the mother–offspring dyad seemed restricted to wound cleaning. In all populations mothers with newborns seem very reluctant to have others touch their infant, but older siblings are sometimes allowed to groom an infant once it is over a few months old. Thus even though allogrooming is rare it does seem to serve a social function in addition to fur and wound cleaning.

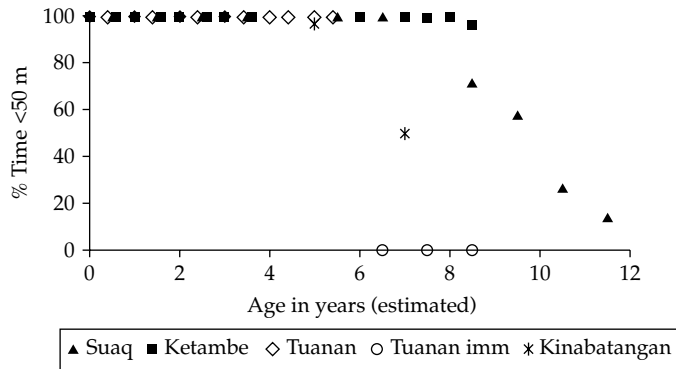
## 12.7 Ranging competence

### 12.7.1 Association with the mother

In the Sumatran study sites, 6–8-year-old offspring tend to stay in almost constant association with their mother, even though they are no longer dependent on her help in navigating the canopy (Fig. 12.3). In both Suaq and Ketambe, 8–10 year-olds finally leave their mothers for longer periods of time, especially when their mother has given birth to a new infant, but they are still seen ‘visiting’ their mother occasionally when they are 11 years old.

The limited data (based on estimated ages) available for Bornean populations suggest a very different picture. There, immatures seem to leave the permanent association with their mothers at an earlier age. In Kinabatangan, one known-aged offspring spent about half the time not in association (>50 m) with his mother when he was 7 years old and his mother had a new baby. Similar patterns were seen for offspring with estimated ages. In Tuanan the oldest immature with known mother, estimated to be 6 years old, already started to leave her mother’s 50 m radius for short periods (hours), rapidly returning to her after scanning the surroundings from a high tree. Half a year later, she was observed to have an overnight ‘excursion’, spending the night near another mother–offspring





**Figure 12.3** The percentage of time offspring of different ages is in association with the mother (<50 m distance) for immatures of four different populations. 'Tuanan imm' represents the three independent immatures who were never seen in association with an adult female likely to be the mother. (Averages as in Figure 12.2.)

pair after extensive play bouts with that offspring, returning the next morning to her own mother >150 m away. Even though the circumstances of this first observed excursion were very similar to ones observed in Sumatra, this immature was clearly younger. Likewise, in Sabangau, one individual estimated to be 4–5 years old would spend considerable periods of time >50 m away from her mother. Six months after these observations were made her mother had a new infant, but the now 4.5–5.5-year-old continued to stay in association with her mother for at least a year afterwards and the mother was never seen to chase her away.

In the Tuanan research area, three 'solitary' immatures were present, with estimated ages of 6, 7 and 8 years at first encounter. None of them was ever seen with a female who could be their mother. Whether or not they were orphans is unknown; however, the two youngest ones were met over a period of at least 2 years and in seemingly good health. These immatures were rarely seen in association with any other individuals (see below). Four similarly 'lonely' young immatures (estimated to be between at most 5–8 years old at first encounter) have been encountered and followed in Sabangau. Three of these were never in association with a likely mother. In addition, in Sabangau one young immature was initially seen in association with a mother with newborn infant, but after a few weeks this immature seemed to be ranging alone most of the time, at a much smaller size (presumed younger age) than observed in the well-known Sumatran populations. In addition, in another swamp forest

in the same province, Sungai Lading, encounters with a single young immature were also recorded occasionally (M.L. Bastian, personal communication). Clearly there is variation between individuals within populations, but overall these data from several Bornean populations suggest that many immatures range entirely independently of their mother at least 2 years, but perhaps as much as 4 years, earlier than their Sumatran counterparts. Obviously, more quantitative data on 6–10-year-old immatures with known mothers are needed for the Bornean populations.

The mechanism of this parting of ways is unknown, and both mother and offspring may be partly responsible. In Suaq, Ketambe and Tuanan, mothers of new infants tended to become less tolerant of their independent offspring when they fed nearby, but less so when they were merely in association. Nevertheless after the disappearance of his 1-year-old sibling, a 9-year-old associated more and even shared his mother's nest again, suggesting that the weaned offspring had an interest in prolonging the association. In Sabangau one mother of a young infant was seen to systematically chase away her weaned offspring, abruptly ending their association, whereas another mother with a young infant tolerated her 5–6-year-old in close association. Likewise, one weaned male immature in Kinabatangan was in peaceful association with his mother and young sibling about 50% of the time when he was estimated to be 7 years old. These observations suggest individual variation or at least variation across specific circumstances.

In summary, available data suggest that in both Sumatra and Borneo offspring start ranging alone around the time of the birth of a younger sibling, although they may still often travel with the mother and their younger sibling for brief periods of time. Overall, then, Bornean immatures seem to leave their mothers sooner, consistent with the observed shorter interbirth interval in Bornean orangutans and the absence of offspring stacking.

### 12.7.2 Social competence

When an immature is no longer in constant association with its mother, it can no longer rely on her to provide protection against conspecifics, but it may also be more able to follow its own preferences in associations. Toward the last phase of lactation, mothers tend to receive increasing attention from males (van Noordwijk and van Schaik 2005). Even though immatures may occasionally have friendly interactions (social play) with such male associates, these are not necessarily their preferred social partners. So, we may expect that association patterns of immatures after they have left their mother more clearly reflect their own preference.

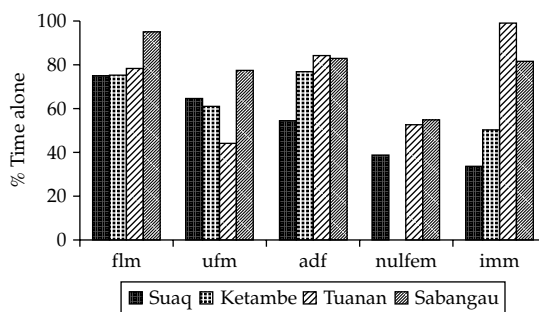
In Suaq, independent immatures initially spent most time away from the mother associating with others, but gradually also spent time alone, with 11-year-olds being without companions for more than half of the time (van Noordwijk and van Schaik 2005). Data from Ketambe indicated a similar pattern (van Adrichem *et al.* 2006). Unfortunately sample sizes per individual are still too small for a detailed analysis of the identity of the partners, although, at first glance, there does not seem to be a major difference with the parties they were in when still accompanying their mothers.

In contrast, in Tuanan and Sabangau (Fig. 12.4), and in Kinabatangan as well, rather young immatures were often encountered without any companions. Even though Bornean orangutans, in general, may seem to be alone more of the time and tend to be in parties of smaller size than Sumatran ones, the difference in sociality for young immatures is more striking than that for any other age sex class (Fig. 12.5). In fact, at least some of the immatures in Tuanan seemed to actively avoid encounters,

even with females with 3–5-year-old offspring who could potentially be play partners.

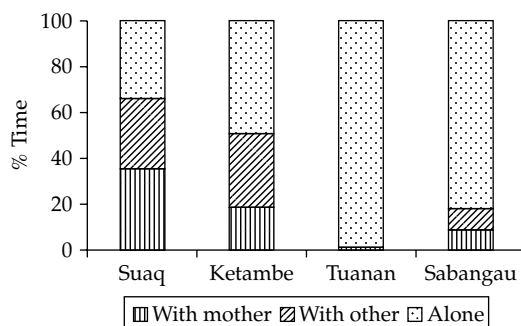
Thus, these immatures seem to lack interest and/or social confidence to form a party with conspecifics.

Some independent, early observations support the notion of a true difference: MacKinnon (1974, p. 51) presents the party compositions he encountered in Ulu Segama (Sabah) and Renun (Sumatra). Although he used necessarily rough developmental classes it is striking that he reports four encounters



**Figure 12.4** The average percentage of time different age classes spend without any independent conspecific within 50 m. Ketambe: data on adult males and females kindly provided by S.A. Wich, data on immatures from van Adrichem *et al.* (2006). Percentages for Suaq, Tuanan and Sabangau based on focal data.

Flm, adult flanged males; ufm, adult unflanged males, adf, adult females, nulfem, adult nulliparous females; imm, independent immatures (i.e. fully weaned and not yet sexually active).



**Figure 12.5** The average percentage of time independent immatures spend in association (<50 m) with their mother (with or without other conspecifics), only other conspecifics or without any conspecifics for immatures in four different sites (data collection as in Figure 12.4).

with a lonely juvenile and two with a juvenile who had only a non-adult female as company in Sabah, whereas in Sumatra, all juveniles he observed were in the company of at least an adult female who could have been their mother. MacKinnon's findings concur with the regular sightings of lonely small immatures in other Bornean sites, in contrast to Sumatran sites. Other pioneering field studies on Bornean orangutans give the same impression of a very low incidence of associations for young independently traveling immatures (Horr 1977; Rodman 1973b). In contrast, Galdikas (1985a, 1995) reported a relatively high occurrence of association for adolescent females (estimated 9–14 years old) in Tanjung Puting and apparently frequent association of immatures with their mother after the birth of a new infant. However, solitary juveniles (estimated 5–8 years old) were also encountered. Obviously, demographic factors will affect whether immatures are able to associate with each other. Nevertheless, it is remarkable that in all Bornean populations for which we have data, immatures are found alone, at least occasionally, at a younger age than in Sumatra. Clearly more longitudinal data on more individuals with known history are required to fully document and understand the more solitary habits of Bornean immatures.

### 12.7.3 Finding food

Detailed analyses of diet selection of mother and offspring in Tuanan showed that an immature is at least familiar with the whole range of its mother's diet before being weaned at around 5 years of age (Massen 2004; Dunkel 2006). As yet, no comparable data are available for other sites, but these results concur with the general impressions from Suaq and Ketambe, as well as Kinabatangan. Thus, except maybe for very rare food sources, weanling orangutans have the experience and knowledge to eat the same diet as their mothers. However, even when immatures are able to eat all foods their mothers eat, this does not necessarily mean that they are also able to find or recognize feeding opportunities on their own. For example, in Tuanan, 3–6-year-old immatures are able to open up rotten pieces of wood to eat termites, but they tend to take pieces of such wood from their mothers

instead of collecting them themselves from the ground or breaking them off from standing dead trees. This probably reflects a lack of competence, because immatures are observed to handle and bite in pieces of rotten wood they pick up, but rarely manage to collect a termite-rich piece. In fact, this is the kind of food over which agonistic interactions between mother and offspring were most frequent (unpublished data). Thus, whereas many necessary food-processing skills seem to be mastered before weaning, recognizing some food items may lag behind. This could explain in part why weaned immatures tend to travel with their mothers for some time after reaching a basic level of processing competence.

### 12.7.4 Range establishment

After the offspring has left its mother and is ranging mostly by itself it is no longer bound to its natal range. The oldest immatures in Suaq (all close to 11 years old: 3 males, 1 female) were still occasionally seen in their mothers' home range, but also in surrounding areas (van Noordwijk and van Schaik 2005). Similarly in Ketambe, with a longer observation history, at least three mature reproductively active daughters are known to have established ranges partly overlapping with those of their mothers. In Tuanan, the one female who has so far matured in the study population did the same. Galdikas (1995) also reports female philopatry for Tanjung Puting. As to males, at least some sexually mature sons (one over 20 years and one at c. 16 years old) in Ketambe are still seen in their natal range, where their mothers are still reproductively active. In general, males' ranges become much larger than those of females (Singleton and van Schaik 2001; Chapter 13 this volume). Thus, the evidence to date from both islands suggests that females settle close to their mothers' range, whereas males range over a much wider area (probably even larger in Borneo than in Sumatra) that may include their natal range as well. Likewise, a recent genetic study of the highly fragmented Kinabatangan population could not find evidence for long distance dispersal of either males or females (Goossens *et al.* 2006b). Ongoing genetic study of both Sumatran and Bornean populations (Krützen *et al.* research

in progress) will soon yield more information on dispersal patterns.

## 12.8 Discussion

### 12.8.1 Do Sumatran and Bornean orangutans differ in development?

Most of the data presented in this chapter are preliminary, for a variety of reasons. First, most research projects have not lasted long enough to cover the development from birth to independence, let alone first reproduction, for any individual. This means that studies generally work with estimated ages. Clearly, age estimates of the younger individuals are more accurate since these are based on comparisons with known-aged immatures born during study periods. The results reported here are different from those reported by the first generation of field studies in the 1970s, because their age estimates of immatures were necessarily based on experience with captive orangutans (Rodman 1973; MacKinnon 1974; Horr 1977; Rijksen 1978; Galdikas 1995). Fooden and Izor (1983) have shown that human-reared orangutan infants grow much faster than even those nursed by captive, well-nourished mothers. Thus age estimates of wild immatures based on any captive-reared ones probably resulted in a serious underestimation. Only long-term studies of wild populations will provide us with hard data on the timing of developmental milestones. All data used here are based on careful age estimates using comparisons of photos taken over several years, although it must be stressed that the age estimates for the Sumatran populations may be more accurate due to longer-lasting study periods than those for the Bornean populations.

Second, sample sizes remain small, and only a much larger sample will enable us to detect systematic sex differences in development under natural circumstances. Observations on reintroduced young orangutans suggested sex differences in skill refinement during adolescence (Russon 2006), but the varied history and social environment of these individuals might have affected these results.

Another potential problem with the current data for a comparison between the island species could be that most of the data on Bornean orangutans come from populations inhabiting peat-swamp

forest, whereas Ketambe, the study site established more than 30 years ago in Sumatra is a dry land forest. Fortunately, developmental data from the orangutan population in the Sumatran peat-swamp forest at Suaq Balimbing suggest a very similar pattern to that from non-swampy Ketambe (van Noordwijk and van Schaik 2005; van Adrichem *et al.* 2006), indicating that a possible effect of habitat is very small.

A final problem with the current data is that for Bornean orangutans we currently have mostly information on *P. p. wurmbii* (Tuanan, Sabangau), a little on *P. p. morio* (Kinabatangan) and none on *P. p. pygmaeus*. Once more data become available for the latter two subspecies we may have to abandon the simplistic Sumatra–Borneo contrasts as used in this chapter.

Despite the shortcomings of the data currently available and the obvious need for further research, we would like to draw attention to some similarities and differences suggested by the current information.

### 12.8.2 Similarities among populations

Infants in all populations are carried by their mothers for the first 2 years of life but take care of most of their own transportation when they are around 4 years old. They still receive occasional help from their mothers in crossing canopy gaps between trees for another 2 years. In both Sumatran and Bornean study populations, 5–7-year-old immatures are competent in negotiating the physical aspects of life in the canopy, although in Sumatra some older immatures are still carried now and again. Well before this age, immatures are competent nest-builders and possess other relevant skills to protect themselves against unpleasant physical environmental conditions. By the time they are weaned, immatures are also familiar with their mother's diet and able to process all food items in their mother's diet. However, their efficiency in food acquisition is still lower than that of older and larger individuals in the population. Contrary to expectation, strength did not seem to be a determining factor in immatures' ability to eat food items (at least in the relatively easy to process diets of orangutans in Tuanan: Dunkel [2006]), although it may still play a role in their efficiency.

Such lack of efficiency may make it uneconomical for small orangutans to harvest some foods, and thus, in populations with a variety of food items that are difficult to acquire, we may well find larger differences with age in actual diets. Data on reintroduced orphaned orangutans do indeed suggest ongoing skill acquisition and increasing efficiencies in regards to complex foraging skills up to at least 14 years of age (Russon 2006).

Even though they presented no quantitative data and had biased age estimates, early studies described a very similar developmental trajectory as we do here, and commented on the long-lasting assistance of the mother in transportation, immatures' nest building competence long before they sleep in their own night nests and the gradual transition from nursing to independent foraging (e.g. Horr 1977; Galdikas and Wood 1990; Galdikas 1995; Galdikas and Briggs 1999).

### 12.8.3 Apparent differences between populations

Despite the major similarities in early development of orangutans in all populations studied, the data suggest an as yet unexplained difference in the timing of final weaning and the end of the continuous association with mother. Even lacking extensive information on known-aged immatures, Bornean orangutans seem to be fully weaned at least 1–2 years earlier than Sumatran ones and appear to leave the permanent association with their mother at a younger age as well. (This age difference also implies that Bornean immatures spend the night in their own nest and thus have to take care of their own thermoregulation at a smaller size than Sumatran ones. The energetic consequences of this difference remain unknown, and may be minor in low elevation populations.) In addition, young independent immatures in the Bornean populations were found to be less gregarious than their Sumatran counterparts.

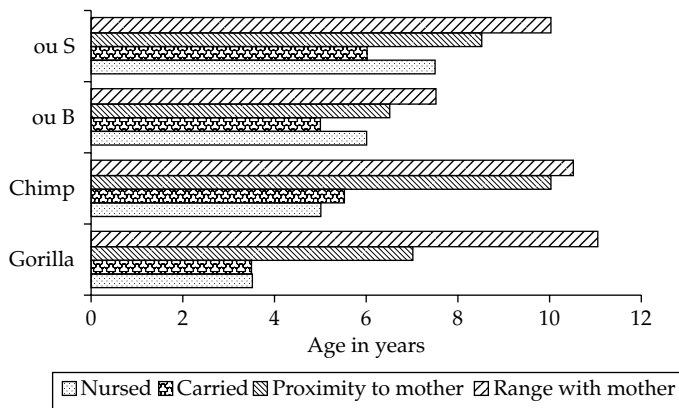
Observations by Horr (1977) suggested that orangutans in Lokan (Sabah) combine a relatively short interbirth interval with a post-weaning association with the mother over several years and thus more overlap between siblings in their association with the mother than known for Sumatra, where association drops below 50% within 2 years of sibling

birth (van Noordwijk and van Schaik 2005). The recent and ongoing observations in Kinabatangan (which is not far from Lokan in Sabah) have confirmed a frequent association of immatures with the mother after the birth of a sibling. However the limited data also suggest that 7–8-year-old immatures spend already more than half their time not in association with their mothers and thus, despite more overlap in association between successive offspring, immatures probably are fully independent at a younger age than those in Sumatra. More detailed observations are needed to assess whether infant stacking could be a feature characterizing *P. p. morio*.

### 12.8.4 Bornean and Sumatran orangutans in great ape perspective

A comparison of the developmental trajectory of great apes (Fig. 12.6), suggests a consistent late age of weaning for both Sumatran orangutans (6–8 years) and Bornean orangutans (5–7 years) as compared to chimpanzees (4–6 years) (Watts and Pusey 1993; Boesch and Boesch-Achermann 2000) and gorillas 3–4 years (Watts and Pusey 1993; Robbins *et al.* 2007). (Unfortunately insufficient developmental information is available on bonobos yet to include them in this comparison.)

Nevertheless, we could find little evidence that late weaning is due to later acquisition of the necessary skill levels needed at weaning: Despite the differences in locomotion between the completely arboreal orangutans and the more terrestrial African apes, orangutans get maternal support during travel (by being carried or assisted in crossing gaps between trees) to about the same age as chimpanzees do (by being carried) (Hiraiwa-Hasegawa 1990a; Tutin 1994; Doran 1997). Food-processing skills and familiarity with at least the maternal diet is acquired before weaning in all apes, although feeding efficiency and special techniques continue to improve up to at least 10 years of age and probably up to the age of first reproduction (Hiraiwa-Hasegawa 1990b, c; Byrne and Byrne 1993; Watts and Pusey 1993; Matasuzawa 1994; Corp and Byrne 2002a; Lonsdorf 2006, Russon 2006). All great apes spend the night in a nest, and immatures are capable of building adequate nests (long) before weaning which usually coincides with the



**Figure 12.6** Comparison between gorilla, chimpanzee, and orangutans from Borneo and from Sumatra: Age until which offspring are nursed, carried, >50% time in proximity to the mother (gorilla: % time <5 m during feeding [Watts and Pusey 1993] chimpanzee: % time <15 m [Pusey 1983]), and >50% of time ranging with the mother.

end of maternal tolerance to nest sharing. Gorilla immatures, which are weaned earliest, seem to be the only apes regularly found sharing the night nest with another conspecific (Stewart 2001; Yamagiwa and Kahekwa 2001). Once orangutans are weaned they continue to spend a relatively short period in the close proximity of their mothers and even start ranging independently at a similar (Sumatra) or earlier (Borneo) age as compared to chimpanzees (Pusey 1983, 1990).

Thus, among great apes, orangutans receive the longest period of unshared proximity to their mother. However, gorillas and chimpanzees are more gregarious and grow up with more exposure to potential additional role models and thus opportunities for social learning. A recent study on a community of rehabilitant Bornean orangutans showed the major role of social learning for the acquisition of the complicated skills needed for successful feeding on a local palm (Russon 2006). However, under circumstances that preclude permanent gregariousness for an arboreal ape, most social learning may necessarily be vertical. It remains to be seen whether the difference in social environment during development will turn out to be reflected in differences in the patterns of distribution of local traditions and innovations.

## 12.9 Conclusion

It has been hypothesized that the solitary lifestyle of orangutans prevents mothers with infants from

permanently associating with their older offspring (van Noordwijk and van Schaik 2005). As long as continued association with the mother contributes significantly to the survival of an offspring it is also in the interest of the mother to maintain this association and even postpone her future reproduction if it would be too costly to combine the two (*cf.* Lee 1986; Dunbar 1988). So far, our interpopulation comparison suggests that, at least for the comparison between *P. abelii* and *P. pygmaeus wurmbii*, there are no major differences in early development. However, the Bornean immatures seem to be completely weaned and subsequently leave the close proximity and permanent association with the mother at an earlier age, and they appear less gregarious. The orangutans studied in the less productive habitats in Borneo as compared to the ones in Sumatra, seem to have opted for shortening the association between mother and offspring instead of prolonging the interbirth interval even further as might have been expected. The mostly qualitative information on *P. p. morio* suggests this subspecies is more similar to *P. p. wurmbii* than to *P. abelii*.

These differences raise the question how and to what extent mothers contribute to the survival and well-being of immatures over 5 years of age (when immatures in all studied populations seem to have acquired basic feeding, locomotory and other skills) and how this differs between the islands. Although few data on the causes of mortality in natural populations are available (see Chapter 5), Bornean populations probably suffer more from

periodic food shortages affecting all individuals in a population (Knott 1998a and Chapter 7). Due to climatic and geographical conditions, such nutritional stress affecting a whole population is less common in Sumatra (Wich *et al.* 2006a). The pilot experiments by Nieuwenhuis (2006) suggest that mothers could have a major positive effect on immature survival by early detection of predators. If the major cause of death for a Sumatran immature orangutan is predation that can be avoided by extra vigilance, then prolonged association with the mother would be beneficial. Similarly, a vigilance benefit of being with conspecifics may also contribute to the more gregarious habits of Sumatran immatures. In contrast, a widespread general food shortage affects both mothers and immatures and thus their permanent association increases energetic stress in both whereas the mother's presence would not significantly reduce the offspring's mortality risk due to starvation. Thus, where a mother cannot significantly protect her semi-independent offspring against its major risks of mortality, she should not postpone her own subsequent reproduction by investing in prolonged permanent association with this offspring, even if there was a marginal (scrounging) benefit to the offspring.

When current conditions are favorable, a mother with a new infant could still tolerate her weaned offspring nearby, but become intolerant as soon as the cost of association becomes too high for her. This may explain the considerable variation found so far in the tolerance and association between mothers and older offspring.

We conclude that a difference between Sumatra and Borneo in the importance of various sources of mortality explains the difference in interbirth interval and age of independence between orangutan populations. Basically, when a mother reaches the point where her full-time proximity and undivided attention hardly increase the survival prospects of her offspring, she is better off ending the costly exclusive association with it and instead she should begin investing in the next one.

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