Social organization and male–female relationships

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Abstract and Keywords
Despite their semi-solitary nature, associations among orangutans are more common than expected by chance for most combinations of age-sex classes. Variation in party size is due to variation in food availability or sexual activity, reflecting the two main types of parties encountered in orangutans. Parties may involve mating or are formed around mothers and immatures of various ages, in which social play is the main social activity. Beyond direct association, Sumatran females tend to remain within audible range of the dominant flanged males, using his long calls to adjust their ranging. Females tend to be more philopatric than males, although it is not clear whether males disperse away from their natal range or end up including their natal range within a much larger home range. The accumulating evidence suggests that orangutans live in more than mere neighbourhoods, but in loose communities in which related females form clusters, share a preference for the same dominant flanged male, within whose earshot they tend to remain and whose ranging is more limited. Further study should reveal whether this Sumatra-derived picture also holds for Borneo.

Keywords: long calls, sociality, home range, associations, food availability, sexual activity, social play

17.1 Introduction
The local social organization of a species refers to the size, sexual composition and spatiotemporal cohesion of its society (Kappeler and van Schaik 2002), assuming there is a society, i.e. a set of conspecific animals that interact regularly and do so more with each other than with members of other such societies. If animals are largely solitary, e.g. because they are territorial or live in overlapping ranges but avoid each other, there is no social organization above the individual or the mother–offspring unit. Their social organization is then best captured
by the term ‘neighborhood’ (Richard 1985), where neighbors know each other well, and know their more distant neighbors less and less. Orangutans are often thought to be the only diurnal primate species that does not show any social units above the level of the individual, resembling some nocturnal prosimians (Bearder 1987; Eberle and Kappeler 2002).

We now know that this characterization is incorrect, at least for well-studied populations in Sumatra. First, adult females regularly form associations with immatures of various ages, fellow females from the same clusters (Chapter 13). Second, they show preferences for associating with particular males that may extend beyond mating itself (Utami and Mitra Setia 1995; van Schaik 1999), suggesting that some function is served by such a tendency. Thus, some orangutan populations appear to have a more complex social structure (the pattern of social interactions and the resulting relationships among the members of a society) than known previously.

In this chapter, we collate what is currently known of female association tendencies and of loose associations between females and locally dominant flanged males at a number of sites in both Sumatra and Borneo. We will then discuss the emerging new understanding of orangutan social organization, and ask whether there are major differences between orangutan taxa.

17.2 Associations
At all sites, animals occasionally congregate when they meet in large fruit trees. At Ketambe, for instance, the large strangling figs often attract multiple adults simultaneously, and up to 14 animals have been seen in or near a single tree. In addition to these passive associations, called feeding aggregations, there are also more active associations, called travel bands by Sugardjito et al. (1987). Associations are more common than expected by chance, as suggested by comparison with ‘gas’ models simulating random movements in a common range (Mitani et al. 1991; van Schaik 1999; Knott et al. in press), even when accounting for degree of home range overlap (Singleton 2000).

Associations may involve sexually active animals, but also involve mothers with immatures and even unflanged males, in which social play is the predominant social activity. However, not all combinations of age-sex classes are equally likely to be
found in association with each other. Sexually active females and unflanged males are rather gregarious, with sexually active nulliparous females being the most gregarious. Non-dominant flanged males tend to be the most solitary because they avoid encounters with dominant flanged males or even the larger unflanged males and are probably in turn avoided by females and immatures.

Mothers with unweaned offspring are on average in association with fewer conspecifics than females unaccompanied by offspring or mothers with (almost) weaned youngest offspring (Fig. 17.1). Not only do potentially sexually active females have more male associates (both flanged and unflanged), they also are more often in association with other females, perhaps because of shared attraction to the same male. Figures 17.1a and b represent the two different clusters of females in Suaq (see also Chapter 13), illustrating variation in social tendencies within a population (see van Schaik et al. 2003b).

This pattern is nicely illustrated by the variation over time in the associates of one female at Suaq, Ani (Fig. 17.2). Ani had a rather large infant, about to be weaned at the onset of the observations in 1994. Unflanged males began to show great interest in her in this year, but she preferred the company of the dominant flanged male(s), whose association with her peaked in 1995, during which she became pregnant in November. During her pregnancy, Ani’s association with both flanged and unflanged males declined, and she began to associate more with mothers and the immatures brought along by her more independent daughter, Andai, who had been weaned the year before. After giving birth, she dramatically increased her association with other mothers, and also still met often with the immatures, until a few years later, the immature bands became less frequent visitors, largely because mother and daughter decreased their associations (cf. Chapter 12).

The data available to date indicate that orangutans at the two Sumatran sites, Ketambe and Suaq, are more gregarious than orangutans at any of the Bornean sites studied to date (Fig. 17.3). Mean party sizes for adult females in Sumatra are between 1.5 and 2.0, whereas on Borneo they tend to be around 1.05 to 1.3 (van Schaik 1999). Party size reflects the mean number of associates for a focal animal, including the
animal itself. Thus, a purely solitary animal would have a party size of 1.0. Dependent infants are excluded from party-size calculations.

There is another curious difference between the islands, concerning independent immatures (Fig. 12.4 in Chapter 12). These are the most gregarious age–sex class at the two Sumatran sites, (p.247)

![Figure 17.1 Average number of associated independent individuals within 50 m of the various age–sex classes for mothers with unweaned offspring vs females without or with older (almost) weaned offspring, at two different sites: Suaq on Sumatra (a. northern females, b.](image-url)
Ketambe and Suaq, but are among the least gregarious classes at the two Bornean sites with quantitative information, Sabangau and Tuanan. This difference may have important consequences. The period of extra gregariousness following weaning allows the young Sumatran immatures to acquire any cultural variants they did not acquire during the intensive apprenticeship with their mother, whereas their Bornean counterparts have fewer opportunities to do this. This suggests that the smaller cultural repertoires of the Bornean orangutans (van Schaik et al. 2003a; see also Chapter 21) may be due to differential opportunities for social learning during the early post-weaning period rather than during the later adult period.

Two major factors are known to affect the tendency to associate: food availability and mating opportunities. Increased food availability eases the (p.248)
costs of association, thus allowing the animals to reap various benefits from sociality, such as social play for immatures and perhaps social learning of skills and information. The frequency of parties that form for these opportunistic benefits may therefore be higher when food is more common, and forming parties may thus not lead to increased travel costs. The island difference is probably due to a difference in food abundance.

On the other hand, when mating opportunities arise association ensues, regardless of food supply, and one would therefore generally expect them to lead to higher costs of association (van Schaik 1999). This is indeed what is found among orangutans: there is no evidence that parties involving mothers cover more distance than lone mothers, whereas flanged males are forced to cover more distance when they associate with sexually active females (Suaq, van Schaik, unpublished data; Ketambe, Utami Atmoko [2000]; Wich et al. [2006b]).

17.3 Male long calls and coordinated ranging
All flanged males emit long calls (Chapter 14), albeit at varying rate (Chapter 15). Here, we are concerned with examining the function of these long calls, by mapping their effects (see Delgado (p.249))
Early ideas were that long calls functioned both in male-male competition and mate attraction (MacKinnon 1974; Galdikas 1984; Utami and Mitra Setia, 1995). Mitani (1985a) concluded that ‘dominant males employ long calls to establish priority of access to any females in the immediate area’. Evidence for the male spacing function (Mitani 1985a) was reviewed in Chapter 15. At least for Sumatran orangutans, the male spacing function faces two challenges. First, subordinate flanged males also emit long calls, and should therefore be at risk of being attacked by dominant males. This either means that they are trying to repel even less powerful males, or perhaps that the long calls also function to attract females. Second, context affects male long-calling rates. Mitra Setia and van Schaik (2007). Because the two studies used slightly different criteria, the numbers are approximate only. At Ketambe, the absolute distance between the calling location and the listener’s location during the time of calling was compared to that 30 minutes later. At Suaq, the angle of movement during the 30 minutes following the call relative to the axis connecting long call location and listener’s location at the time of the call was used to determine the response: less than 45° was called approach, over 90° was called avoid, and between 45° and 90° was called coordinate. To allow for approximate comparability with Ketambe, we added half of the coordinate class to the approach class.
and van Schaik (2007) for Ketambe, and Delgado (2003) for Suaq, show that for 10 of 11 males examined, the rate of long calling is clearly higher when alone than when in association with a female (binomial test, p < 0.01). This finding is difficult to reconcile with a male spacing function, since the need to repel other males is greatest when in association with a female, but instead suggests that the calls serve to attract females, or at least inform them of the male’s presence. Indeed, the highest long-calling rates at Ketambe were when a flanged male had temporarily lost contact with his consort partner (Mitra Setia and van Schaik 2007). Comparing long-calling rates when alone also gave a better fit with male dominance rank, suggesting that males give long calls, despite the risk of being attacked by more dominant males who eavesdropped on the call, because it is their best way to attract females.

There is much anecdotal support for a female attraction function, especially for Sumatra. All (p.250) long-term studies provide examples of females running to flanged males when threatened by unflanged males trying to forcefully mate them (e.g. Galdikas 1985b; Fox 2002; van Schaik 2004; van

![Figure 17.5](image-url)
Noordwijk and van Schaik, unpublished data for Tuanan). The female attraction function makes one strong prediction: females should approach long calls (although females in different reproductive states may do so for different reasons). Recent studies indeed found this to be the case at Ketambe (Mitra Setia and van Schaik 2007) and Suaq (Delgado 2003). Whereas flanged males as a class avoid male long calls, females, as a class, approach them, being significantly closer to the male’s calling location 30 minutes after the call than they were at the time of the call (Fig. 17.4). The female tendency to approach the male long call does not depend on their reproductive state (Mitra Setia and van Schaik 2007); females with or without dependent infants are equally likely to approach, even though that approach usually does not need to lead to actual association. The data from Ketambe indicate that females selectively approach after long calls by the current dominant male (Fig. 17.5), rather than those of the recently deposed male, even to within association distance and association time from follow data (Mitra Setia, unpublished data). There are no published data yet on the responses by unflanged males to long calls.

It should be stressed that approaching a long call does not necessarily mean that the females end up actually associating with the male. Indeed, in most cases they do not. Instead, selectively approaching long calls by particular males should allow females to maintain earshot associations, i.e. stay within audible distance of calling males (Mitra Setia and van Schaik 2007). This is made possible by a subtle tactic of the calling male: after calling in a particular compass direction, he subsequently travels in approximately that direction for several hours (L. Damerius, R. Delgado and C. van Schaik, in preparation). Thus, when a female approaches a long call especially when the male appears to be far away, either because he is indeed far away, or because he appears to be far away (because he is facing away from the female as he calls), she is more likely to remain within earshot of this male.

For Suaq (Fig. 17.6), simultaneous follows of females and flanged males in the same study area (and excluding all data when male and female were in consort) allow us to calculate the distribution of distances between various pairs of individuals. These data show that the average distance of a Suaq female to the then-dominant male, Arno, is far smaller than that to the other flanged males (average of several
males), even though both are present in the study area. To put it quantitatively, if the average maximum hearing distance of long calls is about 1 km (depending on the male’s calling direction), then a female at Suaq is within audible range of Arno over 90% of the time, and within audible range of any other male in the same area for around 70%. On average, a female is at c. 550 m from Arno and c. 730 m from any other flanged male. This suggests that females at Suaq are able to stay within earshot of Arno most of the time, probably through the responses to his long calls documented above.

These results, taken together, show that Sumatran females, regardless of their reproductive state (and perhaps others as well), use the long calls of individually known males generally to achieve

![Figure 17.6](image)

**Figure 17.6** Cumulative distribution of the distance between adult females and either the locally dominant male, Arno, or any of the other flanged males in the area, at Suaq. Based on simultaneous follows, but excluding consort pairs (Singleton and van Schaik, unpublished data). Note that females are on average closer to Arno than to other flanged males. Sample size refers to number of 30-minute points at which coordinates were recorded.
coordination, i.e. they approach to some extent but usually not to within visual contact. Thus, male long calls serve primarily to attract females. The female responses suggest that they are trying to maintain earshot associations with the locally dominant male, although more precise studies are needed. The function of these loose associations is almost certainly that they allow females to seek refuge with the flanged males, especially dominant ones, if they are being harassed by other males. However, many more detailed observations and analyses are needed to demonstrate this function beyond doubt.

There is little information from Borneo, apart from the observation that long calls serve the male spacing function (Mitani 1985a) and that harassed females sometimes rapidly approach long calls (Galdikas 1985b; Tuanan project, unpublished data). However, preliminary data from Tuanan suggest that there is at least variation between populations in the relationships between flanged males. Even after 4 years of study the rank order among all sighted flanged males is not yet obvious to the human observers, not in the least because no single male has been consistently present over these years. It remains quite conceivable that the social organization on Borneo is different, or at least variable among sites, and that the idea of earshot associations, confirmed for Sumatra, does not hold there.

17.4 Philopatry and dispersal
Although individual studies generate only very small sample sizes, all behavioral studies suggested that many maturing females settle near their mother's home range (female philopatry) and that males disperse (Rodman 1973b; MacKinnon 1974; Rijksen 1978; Galdikas 1985a; Mitani 1989; van Schaik and van Hooff 1996; Singleton and van Schaik 2002). A striking example of female philopatry is found in Ketambe, where the daughters and granddaughters of the reintroduced rehabilitant female Binjai all settled in the study area. These observations agree with the idea that females form clusters of relatives, who have more tolerant social relationships, in that they meet more often, show less aggression, and show feeding tolerance. Nonetheless, new females are occasionally encountered in long-term study sites, although this is consistent with a philopatric tendency if these females shifted their range somewhat, rather than vacated it and moved away to a new one. Similarly, males seemed to disappear, although recognition of maturing males that may be absent for a long time may be difficult. Maturing males seem
to visit their mother’s range for years after the end of permanent association (see Chapter 12), consistent with an expansion of range including natal area at least initially – instead of radically moving away as in natal emigration by cercopithecine monkeys (Pusey and Packer 1987).

Using genetic markers may make it possible to reassess this impression. Utami et al. (2002) estimated relatedness based on eight microsatellites, and concluded that the males in the Ketambe study area were non-related, and in some cases even emanated from different populations, suggesting long-distance dispersal. The mean relatedness among females was also somewhat negative, suggesting mixing of populations, but this can be accounted for by the introduction of two rehabilitant females (including Binjai, mentioned above) into the population during the late 1970s.

In contrast, the study by Goossens et al. (2006b) in Kinabatangan, estimated relatedness based on 14 microsatellites. They found that the mean relatedness among resident females was high ($r_{xy} = 0.303$) and the same as that among resident males ($mean r_{xy} = 0.305$). While this is expected for females if they form clusters, it is surprising for males, who were expected to show lower relatedness if they move away from their natal area and settle elsewhere. Moreover, this study also showed that resident females were more related to each other and to the resident males than they were to non-resident females, and that resident males were more related to each other and to the resident females than they were to non-resident males.

This pattern can be interpreted as indicating limited dispersal away from the natal range, and may therefore reflect the fragmentation that has taken place in the Kinabatangan floodplain over the past 50 years (Ancrenaz et al. 2004a; Goossens et al. 2005a, 2006a). Lot 2 of the Kinabatangan Wildlife Sanctuary, which comprises the study area, is surrounded by oil palm plantations and further fragmentation by drains, small rivers, roads and villages might prevent males from dispersing. On the other hand, the data are also consistent with a slightly different pattern of male dispersal. Males may merely extend their range in all directions, while still including their former natal range as a small part within their new range. In that case, mean relatedness among males will tend to be low as well, but there should be the occasional
high relatedness between particular male–female dyads. This kind of male dispersal may be common among marine mammals, in which discrete ranges are absent (e.g. Krützen et al. 2004). New data are needed to distinguish these two models.

17.5 Orangutan social organization revisited
The traditional textbook characterization of the orangutan's social organization is as follows. Females are solitary, except for brief periods of consortships when they are ready to conceive. Although they live in home ranges that show some overlap, they avoid each other. The fiercest flanged males are territorial, whereas the smaller flanged males and unflanged males (both sexually mature) quietly and inconspicuously roam around large areas and sneak through these territories, avoiding encounters with these highly intolerant, territorial, resident males. There are no social bonds among females, no male–female relationships beyond mating and fundamental intolerance and avoidance among males.

Recent results suggest that at least some aspects of this characterization, based on some early short-term studies, are ripe for reappraisal, certainly for Sumatra but also for (some) Bornean populations. The evidence presented in the chapters in this section of the book suggests the existence of loose communities, organized around a dominant flanged male, as first suggested by MacKinnon (1974). First, at least in some sites females appear to form clusters of presumably related females, with high home range overlap, and (relatively) high frequency of association with fellow cluster-members (Singleton and van Schaik 2002; Knott et al. in press; Chapter 13). Second, one flanged male is dominant and his range is more restricted than that of others (‘resident’), at Ketambe (te Boekhorst et al. 1990; Chapter 15) and Suaq (Singleton and van Schaik 2001; van Schaik 2004). Third, this male also seems to be the favorite mating partner of parous local females, who tend to avoid associations and matings with the unflanged males and the non-dominant flanged males (Chapter 16). Fourth, females tend to remain within audible range of this male, even if they are not receptive, perhaps to avoid harassment by other males (this chapter; see also Fox 2002). Finally, this loose community may move around seasonally,
creating the pattern of seasonal absence and presence recorded by te Boekhorst et al. (1990; cf. Mitra Setia, 1995).

It was noted at several sites that adult females were rarely encountered in some parts of the study areas, or adjacent areas that were occasionally checked. In these areas, however, one tends to encounter adolescents, non-dominant flanged males in poor condition, and/or unflanged males. At Suaq, for instance, these ‘overflow’ areas were the deeper swamps and the hills (both less productive), and at Ketambe, they were the highest zones in the study area. The presence of these overflow areas explains why dominant males tend to be most present in our study areas, i.e. the areas with high female density. Thus, the social landscape of orangutans, viewed at a somewhat larger scale, contains noyeaux of higher female density and a special subset of the other age-sex classes, whereas the areas in between contain a biased set of socially marginal individuals. TMS also suspects that flanged males are less likely to give long calls when in these overflow areas.

The high-female density areas may correspond to the ‘arenas’ recognized by Rijksen and Meijaard (1999). Their term suggests the presence of leks, in which flanged males accumulate and to which females are attracted when receptive. There is no evidence that flanged males accumulate anywhere, nor that females leave their regular home ranges to search for flanged males in a specific area, although they tend to range more widely during periods of sexual activity (van Woerden et al. 2007).

Further study must reveal the generality of the community organization pattern found in the well-known Sumatran sites. Elements are likely to differ (p.253) and vary on Borneo. For instance, in some Bornean sites, such as Tanjung Puting (Galdikas 1985a, b) or Tuanan (unpublished data), a dominant flanged male, even when one can be recognized, does not seem to limit his ranging to a smaller area. Vocally mediated earshot associations are therefore expected to be absent as well, which might also explain the higher levels of harassment at several Bornean sites (see Chapter 16).

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