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Female philopatry and its social benefits among Bornean orangutans

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Abstract Female philopatry in mammals is generally associated with ecological and sometimes social benefits, and often with dispersal by males. Previous studies on dispersal patterns of orangutans, largely non-gregarious Asian great apes, have yielded conflicting results. Based on 7 years of observational data and mitochondrial and nuclear DNA analyses on fecal samples of 41 adult Bornean orangutans (*Pongo pygmaeus wurmbii*) from the Tuanan population, we provide both genetic and behavioral evidence for male dispersal and female philopatry. Although maternally related adult female dyads showed similar home-range overlap as unrelated dyads, females spent much more time in association with known maternal relatives than with other females. While in association, offspring of maternally related females frequently engaged in social play, whereas mothers actively prevented this during encounters with unrelated mothers, suggesting that unrelated females may pose a threat to infants. Having trustworthy neighbors may therefore be a social benefit of philopatry that may be common among solitary mammals, thus reinforcing female philopatric

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tendencies in such species. The results also illustrate the diversity in dispersal patterns found within the great-ape lineage.

Keywords Male dispersal · Female philopatry · Pedigree · Female–female association · Range overlap · Social play

Introduction

In most mammals, females show philopatry, i.e. settle for life in or near the area in which they are born, whereas males disperse (Greenwood 1980; Waser and Jones 1983; Pusey and Packer 1987; Lawson Handley and Perrin 2007). Philopatry has ecological advantages in that it enables the individual to continue to live in a familiar habitat and maintain a familiar diet, without having to experience the costs in terms of time, travel, and risk of finding a suitable area in which to settle. In addition, philopatry may enable individuals to maintain lifelong supportive social bonds with known relatives. In group-living primates, for instance, philopatric females tend to live in close association with their maternal relatives, who may provide mutual support in conflicts with less-related group members (e.g., Silk et al. 2009; 2010; see also Holekamp et al. 2012 for a similar system in spotted hyenas). Likewise, elephants living in fission–fusion female groups maintain supportive social relationships and show preferential associations with their matrilineal relatives in or near their natal range (De Villiers and Kok 1997; Archie et al. 2006). Thus, philopatry may bring social as well as ecological benefits. On the other hand, philopatry may limit access to unrelated and willing mates. Thus, in general, if members of one sex derive a clear advantage from being

(more) philopatric, the other sex tends to derive a reproductive benefit from moving further away (Bengtsson 1978).

For species with strong ecological pressure on females to be more or less solitary, the social advantage of their philopatry is likely to be reduced, and therefore the tendency for female philopatry may be relaxed. Nonetheless, genetic and radio-telemetric research has confirmed that females in many non-gregarious mammal species settle in home ranges adjacent to, or overlapping with, their natal range and thus their female kin (e.g., tigers, Smith 1993; raccoons, Ratnayeke et al. 2002; bears, Støen et al. 2005; Moyer et al. 2006; woodrats, McEachern et al. 2007).

One possible explanation for the philopatric tendency of females in solitary mammals is that the ecological benefits on their own are strong enough to favor female philopatry, especially in species where males have much larger ranges than females and do not derive reproductive benefits from remaining philopatric. Where males derive strong benefits from philopatry, for example through coalitionary defense of a range or access to females, the less gregarious females are likely to disperse (e.g., chimpanzees, Langergraber et al. 2007; spider monkeys, Di Fiore et al. 2009). However, it is also possible that "solitary" females in many species do accumulate social benefits, which accrue at rare but critical times in the life cycle. Indeed, there is evidence that, in some solitarily foraging species, females may be temporarily gregarious when they have dependent offspring. For example, females of the nocturnal mouse-lemur, *Microcebus murinus*, may share a nest hole for their young and even allo-nurse each other's young. Only closely related females have been observed to share in this way, thus both gaining foraging efficiency and maybe increased survival of their offspring through better thermoregulation and increased chances of adoption (Eberle and Kappeler 2006; cf. König 2006 for house mice). Some bats also associate at the roost preferentially with close maternal relatives during lactation, mutually gaining thermoregulatory benefits during a period of high energetic demands (Kerth et al. 2002). These observations raise the question whether social benefits are more common than usually assumed, which would strengthen a female philopatric tendency even in largely solitary species. Unfortunately, for most species it is unclear whether and how females interact differently with their related neighbors compared to unrelated ones, and thus whether they derive social benefits from philopatry at some stage during their lives.

Sumatran (*Pongo pygmaeus*) and Bornean (*Pongo abelli*) orangutans are the only ape species in which both males and females are habitually non-gregarious, like in many non-primate mammals. Especially the Bornean species shows a strong tendency towards solitary life (van Schaik 1999; van Noordwijk et al. 2009). This solitary lifestyle suggests that advantages for either sex of philopatry would be limited to the ecological advantage of familiar range and diet, unless unexpected social benefits are present. For this reason it is interesting to assess the degree to which females or males remain philopatric, and relate these tendencies to a detailed study of their social behavior.

Another reason for interest in orangutan philopatry patterns is that they are one of our closest living relatives. In chimpanzees, males are found to be the more gregarious sex and to be strongly philopatric, allowing them to form long-lasting bonds with their relatives, whereas females tend to disperse from their natal community (Langergraber et al. 2007). In another close relative, the gorilla, females as well as males usually disperse (e.g., Douadi et al. 2007; Robbins et al. 2009), whereas males in Eastern gorillas males may occasionally "inherit" the groups in which they are born (Watts 2000; Bradley et al. 2007). Thus among the extant African apes at least female-biased dispersal seems to be the dominant pattern and has been proposed to be the tendency in the last common ancestor of humans and African apes (Ghiglieri 1987). Although various authors have assumed that female dispersal is a deeply rooted hominoid tendency (e.g., Foley and Lee 1991; Hrdy 2009; Chapais 2010), the "natural" human dispersal system has remained a topic of debate (Hill et al. 2011). Therefore, establishing the natural dispersal pattern of the orangutan may provide a broader perspective to the reconstruction of the origins of the various dispersal patterns found within the hominoid lineage.

Long-term field observations on orangutan populations on both Sumatra and Borneo indicate that adult males have very large overlapping ranges, but rarely associate with each other (Galdikas 1985; van Schaik 1999; Utami Atmoko et al. 2009), and concentrate their associations with females largely to the periods in which these are potentially fertile. There is no evidence for male social bonds, as in chimpanzees, and thus male philopatry is not expected. Females have smaller ranges than males (Singleton et al. 2009; Utami Atmoko et al. 2009), which can also largely overlap, and they spend most of their time accompanied only by their dependent (and sometimes one semi-dependent) offspring (van Noordwijk et al. 2009). For Sumatran orangutans, Singleton and van Schaik (2001; 2002) found clusters of females who associated more often with each other than expected based on their (extensive) range overlap. If females from the same cluster met, they were also more tolerant of close proximity than when females of different clusters encountered each other. These authors hypothesized that such female clusters were based on relatedness, thus implying female philopatry with some social benefits, but lacked the genetic data to verify this. On the other hand, Knott et al. (2008) emphasized for a Bornean population (Gunung Palung) that females show active avoidance of other females within their overlapping ranges, even though assumed relatives had more frequent encounters. In addition, they

concluded that the outcome of a female-female encounter depended on its location relative to the females' respective core areas and thus that females defended their ranges. Thus, although female philopatry may be present in both orangutan species, social benefits appeared to be modest at best among Bornean orangutans.

Behavioral studies on maturing individuals have suggested a tendency towards female philopatry and male dispersal in orangutans of both islands (van Schaik and van Hooff 1996). However, the first studies that estimated genetic relatedness patterns among males and females in several populations have reached divergent conclusions, ranging from both sexes dispersing equally (Utami et al. 2002) to being equally philopatric (Goossens et al. 2006) to male-biased dispersal with female philopatry (Morrogh-Bernard et al. 2011). Nevertheless, recent population genetic analyses using both mitochondrial DNA and Y-chromosome markers indicate a spatial structuring congruent with male dispersal over large distances and very restricted female dispersal for both species (Arora et al. 2010; Nater et al. 2011; Nietlisbach 2009).

The aim of the present study was to use a combination of genetic, ranging and socio-behavioral data of individuals in an intensively studied population of orangutans (*Pongo pygmaeus wurmbii*) in Tuanan (Central Kalimantan, Indonesia) to assess for this population (a) whether females and/or males are philopatric or disperse and (b) whether philopatry was accompanied by social advantages. The genetic analyses focused on detecting mother–adult offspring dyads based on mitochondrial and nuclear DNA (Arora et al. unpublished data). Given the stability of adult females' ranges (e.g., Wartmann et al. 2010 for the same population), the mother's range is the best estimate of any adult individual's natal range and thus maternal relatedness among adults is essential for documenting dispersal patterns.

Materials and methods

Study population

The Tuanan Orangutan Research Area (2° 09′ South; 114° 26′ East) is located in formerly selectively logged swamp forest on shallow peat (<2 m) in the Mawas Conservation Area, Central Kalimantan, Indonesia. The orangutan population here has been studied since June 2003 and has approximately 4.5 individuals per square kilometer (van Schaik et al. 2005). Individuals born before the start of the observations were assigned to age–sex categories based on prior experience (cf. Wich et al. 2004). The study area of ca. 750 ha (gradually enlarged to >1,000 ha) encompassed several complete ranges of adult females, but ranges of all known males extended beyond this limited area. In this

population, adult females spent on average less than 20% of their time in association with another adult conspecific (van Noordwijk et al. 2009).

Observations in the field followed the standardized orangutan protocol (see www.aim.uzh.ch/orangutannetwork). Analyses on adult female ranging, association pattern, activities and social interactions are based on more than 16,650 h of focal observation on 8 different mothers collected by a well-trained team of observers from July 2003 to July 2010. Most data were collected during nest-to-nest follows lasting a maximum of 10 consecutive days per month per focal female. During nest-to-nest follows, observation time was counted from the moment the focal female left her night nest in the morning until she rested in a (new) night nest in the evening (average active time per day for adult females was 10 h 50 min; $N=1,330$).

Adult female home ranges were found to be highly stable over time (Wartmann et al. 2010). Here we included data on adult females (who had at least 1 offspring and were habituated to human observers) if in total at least 250 h of focal observation and ranging data were collected for that female (thus excluding 5 known adult females ranging at the periphery of the study area). For each dyad of females, only those data collected during the same years were used for a dyad-specific sample (resulting in different sample sizes per dyad—see supplemental Table 1). All but one focal female had a dependent unweaned offspring (i.e. <7 years old) for at least part of the data collection period, and three focal females were accompanied at least part of the time by a young infant as well as a weaned offspring. In total the regular focal females had five female and four male immature offspring.

Sightings of all identified individuals were recorded for each month throughout the study period. The percentage of months an individual was present in the study area was based on focal follows as well as sightings during focal follows of other individuals or other research activities in the forest. Observational data on males were collected in the same way as for females. In total, over 10,500 h of focal data was collected on those males sighted during at least 10% of the observation months. Data for the two morphs of adult males are presented separately, i.e., for flanged (with full secondary sexual characteristics, including cheek flanges) and unflanged males (without such characteristics, but capable of siring offspring under natural conditions: Utami et al. 2002; Goossens et al. 2006). All young adult males are unflanged, but the age at which an individual male develops flanges is probably highly variable (Utami Atmoko et al. 2009).

Genetic analyses

We evaluated the maternal relatedness of individuals at the study site through maternity analyses and inference of

maternal siblings, using biparentally inherited microsatellite markers and a maternally transmitted mitochondrial DNA (mtDNA) marker. Fecal sample collection and storage was carried out using a standard genetic sampling protocol http://www.aim.uzh.ch/orangutannetwork/GeneticSamplingProtocol.html, followed by the generation of data on autosomal microsatellites and mitochondrial DNA (mtDNA; details in Arora et al. 2010). We verified that the samples belonged to distinct individuals by genotyping them at six microsatellite markers, which had a combined non-exclusion probability of 1.36×10^{-5} and 8.90×10^{-3} for unrelated individuals and full siblings, respectively, as calculated in Cervus 3.0 (Kalinowski et al. 2007). This procedure identified 47 unique individuals. For 41 of these individuals we generated genotypes at an additional panel of 18 loci, totaling 24 autosomal microsatellite markers. For six males low DNA quantity and quality did not allow us to complete the genotyping for all loci. Thus, for these males, only the identification panel of six markers was used, which in combination with the use of mtDNA markers was sufficient to exclude all but one mother–son dyad (Arora et al. unpublished data)

To identify mother–offspring pairs, we carried out maternity analyses using the likelihood approach implemented in Cervus 3.0 (Kalinowski et al. 2007), using the strict 95% confidence level. All individuals were assessed as potential offspring, but only sexually mature females were incorporated as candidate mothers. To determine critical values of the log-likelihood score for a 95% confidence parentage assignment, we ran 10,000 simulations with the following parameters: a minimum of 6 loci typed, and our genotyping error rate of 0.112% (Arora et al. unpublished data) as empirically determined through the "repeat-genotyping" and "unintentionally re-sampled individuals" approaches described by Hoffman and Amos (2005). The proportion of candidate mothers sampled was difficult to estimate from field data. It has been shown that this parameter may have a substantial influence on the statistical significance of the parentage assignments (Krützen et al. 2004). Thus, we tested several conservative values (0.05, 0.08, and 0.10) and corroborated that the results were robust. In all cases, mother–offspring dyads detected using microsatellite data, also shared their mtDNA haplotype. In addition, all known mother–unweaned offspring dyads, with samples available for both ($N=8$), were confirmed to have a genetic mother–offspring relationship according to our procedures. Individuals sharing a mother were inferred to be maternal siblings. A limitation to this approach is that individuals that are maternally related may not be detected due to the absence of (a sample of) a shared mother. However, this bias is not expected to differ for females compared to males. For all further analyses, maternally related dyads were defined as either a mother–offspring pair, or two individuals sharing a mother.

Ranging behavior

The ranging behavior of 8 focal females was investigated at the level of both home range and core range areas to obtain estimates of proportional dyadic overlap. Using locational data collected at 30-min intervals (see criteria for inclusion above), the respective ranging areas of all females were calculated on a dyad-specific basis. We delineated home ranges by 95% volume isopleths (Anderson 1982) on utilization distributions obtained from fixed Gaussian kernel density estimation (using BCV to estimate the kernel's bandwidth; Worton 1989), whereas core areas were defined by 50% volume isopleths. Areas of overlap were subsequently calculated and divided by the dyad-specific home range area of each focal female. This resulted in an asymmetric matrix for both proportional home range and core range overlap of 52 of the 58 possible dyads (insufficient concurrent ranging data were available for 6 dyads). All analyses on ranging behavior were conducted using the HRT plug-in (Rodgers et al. 2007) and Spatial Analyst extension for ArcGIS 9.3 (ESRI 2008).

Association and social interaction analyses

Whenever 2 individuals approached to within 50 m, this was considered an encounter. Encounter rates were based on the number of new approaches within 50 m occurring during a focal follow starting at the morning nest. If a dyad had spent the night within 50 m of each other, the (continuing) association the next morning was not counted as a new encounter. The percentage of time in association (<50 m distance) was based on total active time from the focal female's perspective. The relationship between time in association and range overlap between two females was based only on those years for which ranges for both could be calculated. When individuals were simultaneously feeding in the same food source <10 m apart they were said to show "feeding tolerance." An agonistic interaction was defined as one in which one individual shows clear aggressive acts such as slapping, grabbing, biting or a fast chase and/or the other shows obvious avoidance or submissive behavior such as fleeing fast (through canopy or over the ground) or screaming. In the analyses, social play among offspring of different mothers could include both unweaned and weaned offspring as long as these were in permanent association with the mother.

Unfortunately, as in previous studies on wild orangutans, the small number of mother–offspring dyads did not allow for an analysis of the effect of offspring sex (van Noordwijk et al. 2009). However, so far, no striking differences between female and male dependent offspring in time budgets or social interest have become apparent.

Statistical analyses

Given that dyadic data are inherently non-independent, permutation versions of standard statistical techniques were employed in which significance of test-statistics was assessed by 10,000 randomizations. To test whether the degree of overlap in ranging areas (both at the home and core range level) differed between related and unrelated female dyads, permutation unpaired t tests were conducted (Legendre and Legendre 1998). Differences in the duration of association among dyads were compared in a permutation one-way ANOVA test (Legendre and Legendre 1998). Post hoc pairwise comparisons (Tukey's honestly significant difference tests) subsequently revealed which categories of dyad were significantly different from each other. Potential associations between overlap in ranging areas and encounter frequency and association time were considered separate for unrelated and related female dyads by computing Pearson permutation correlation tests. Differences in the encounter frequencies and duration of association between unrelated and related female dyads were investigated in more detail by a permutation unpaired t test.

Results

Genetic analyses

In total, 10 different mtDNA haplotypes were found for the individuals sampled in Tuanan. All females (including all additional adolescent and nulliparous ones) had one of only three haplotypes; whereas for the males, eight different ones were found. Only one haplotype was shared by males and females. This distribution of haplotypes was significantly different for females and males (Arora et al. unpublished data).

Pedigree analysis based on nuclear and mtDNA indicated the presence of one mother with three adult daughters (for which maternal sibship was thus inferred) and one mother–adult daughter dyad, all with ranges mostly inside the study area. In addition, 2 independently ranging adolescent females could be matched with their mothers ranging in the periphery of the study area. In contrast among the 28 males, only 1 young one (estimated 10–15 years old) could be matched with his peripherally ranging mother. Thus, both the much greater concentration of females in a few haplotypes and diversity of haplotypes of the males and the sex difference in the presence of dyads of maternally closely related adults in the study area are consistent with greater female philopatry and male dispersal.

In the following sections we refer to the 4 genetically detected mother–adult daughter dyads as well as the 3 female–female sibling dyads (based on sharing the same mother) as "related dyads" and all other female–female dyads as "unrelated dyads."

Spatial analyses

Male ranges and overlap

None of the known adult males had his complete range within the study area. In addition, most of the known males were seen throughout this area. Thus, male ranges were estimated to be considerably larger than even the expanded study area of 1,000 ha. In addition, all known males were regularly observed to leave the study area. Only 1 (flanged) male was sighted during ca. 50% of the observation months (compared to 4 females during >75% of the months), whereas 13 additional males (7 flanged; 5 unflanged) were sighted during at least 10% of the months (the other 14 genetically identified males [11 flanged and 4 unflanged] were sighted less often). These observations suggest major home range overlap among the many adult males sighted in the area.

Female ranges and overlap

Some females could never be followed for more than a few consecutive days before they left the study area, whereas others never travelled outside of the study area during follows. In the analyses of home range overlap we only included those females for whom we were confident to have adequate data to calculate their 95% and 50% use area, based on 1–8 years of data per dyad. Overlap was always calculated from the perspective of the focal female (resulting in 2 different values per dyad). The average home range size for females with ranges inside the study area was 327.5±124.7 ha, with a core area (50% use) of on average 84.0±27.6 ha.

All known maternally related female dyads had overlapping home ranges (Fig. 1; average HR overlap per dyad: 57.32%, N=12), as well as overlapping core areas (average 15.79% (Fig. 2a). Within the study area, non-related female dyads (N=40) had an average overlap of 36.90% and core range overlap of 6.85%, which is significantly less (home range overlap: permutation t test, $t_{(50)}=2.51$, $P=0.015$, $N_{perm}=10,000$; Core range overlap: permutation t test, $t_{(50)}=2.25$, $P=0.027$, $N_{perm}=10,000$). However, more than half of the unrelated dyads (N=23) exhibited a degree of overlap equal to or greater than the minimum observed overlap between related dyads (32.1%), and when comparing these (average 54.04% HR overlap and 10.76% CR overlap) to related dyads, differences were no longer significant; permutation t test for HR overlap: $t_{(33)}=0.466$, $P=0.65$; CR overlap $t_{(33)}=1.029$, $P=0.32$. Thus matrilineal clusters of females have overlapping ranges, but home ranges and core areas may be shared with unrelated adult females as well, and to a similar extent.

Fig. 1 Map of the overlapping home range areas (95% use) of 7 focal females calculated for 2008. Females Jinak, Juni, Kerry, and Mindy are members of the same matriline; Desy is the daughter of Inul, and for Talia, and Sidony no matrilineal adult female relatives are known. Also indicated are the parts of the home ranges of the additional females Wilma and Tina (probably maternal relatives, but not mother–daughter) and Pinky for as far as they are known in the study area. The research station is indicated with a *flag*. (The area to the west of the study area is burnt and severely degraded habitat)
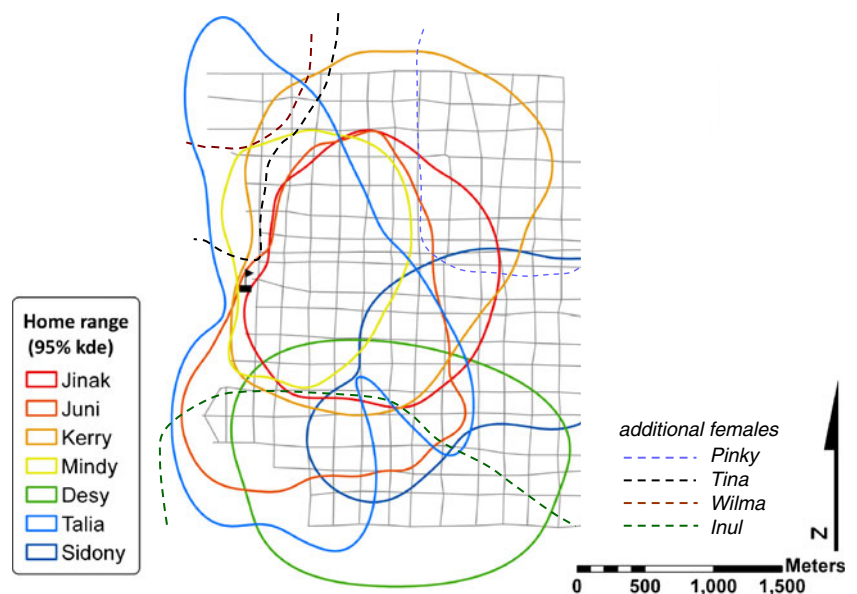
Social relationships

Male–male social relationships

During 7 years of focal sampling on adult males, male–male encounters and associations were rare. Flanged males spent on average 0.11% of their focal time in association with another flanged male, flanged with unflanged males on average 0.25%, and unflanged with unflanged males 3.12%, but only 1.0% when they were not also in association with an adult female. Associations among male dyads of all combinations lasted significantly shorter than those among closely related females, but were not different from those of unrelated females (permutation one-way ANOVA: $F=20.70$, $P=0.0001$; post hoc pairwise comparisons—Tukey's HSD—reported in Supplementary Table 2).

Only unflanged males occasionally showed feeding tolerance towards other unflanged males (at least briefly during 26% of unflanged male associations, or 8% of all male–male associations). Social play among two unflanged males was observed during five associations—(four times involving the same male with three different partners) and except for one event such play lasted only for a few minutes. No grooming or coalitions against another individual were ever observed among males and only one association between unflanged males was continued the next morning (see also Supplementary Fig. 1). Thus, we found no evidence for any special relationships, social bonds or coordinated ranging behavior among adult males in this population.

Female social relationships

Female encounters and associations The frequency of encounters amongst female dyads was not related to the percentage of home range overlap (permutation correlation test: related dyads: $r_{Pearson}=-0.22$, $N=12$, $P_{perm\ (n=10,000)}=0.49$; unrelated dyads: $r_{Pearson}=0.19$, $N=40$, $P_{perm\ (n=10,000)}=0.24$). Even degree of core range overlap was not significantly correlated with encounter frequency among related dyads ($r_{Pearson}=-0.16$, $N=12$, $P_{perm\ (n=10,000)}=0.62$), whereas it was positively correlated for unrelated dyads ($r_{Pearson}=0.41$, $N=40$, $P_{perm\ (n=10,000)}=0.019$). However, if we only consider those unrelated dyads with a total home range overlap equal to or greater than the minimum observed amongst related females, there was only a trend ($r=0.34$, $N=23$, $P_{perm\ (n=10,000)}=0.09$).

Overall, females encountered their close maternal relatives more often than other females with similar degree of home range overlap, i.e., those unrelated dyads with an overlap of more than the minimum among related dyads of 32.1% (permutation unpaired t test: $t=6.49$, $N_1=12$, $N_2=23$, $P=0.0001$). This distinction between relatives and other females is also reflected in the percentage of time focal females spent in association with other adult females (Fig. 2b; $t=5.59$, $N_1=12$, $N_2=23$, $P=0.0001$). Additional analyses of encounter rate and association duration divided by percentage home range and core range overlap respectively, yielded also very significant differences between related and unrelated dyads (Fig. 2c).

Once associations occurred, their duration among related females was also longer than among non-related females (Supplementary Table 2). In addition, none of the 37 observed associations between unrelated females lasted for more than 3 h and none was maintained overnight, whereas 96 of 194 (49.7%) associations of related females lasted more than 3 h, and in 54 out of 194 (27.8%), a night nest was made within 50 m of each other. This bias in both encounter frequency and association time strongly suggests that spending time in association is an active choice and not a by-product of range overlap.
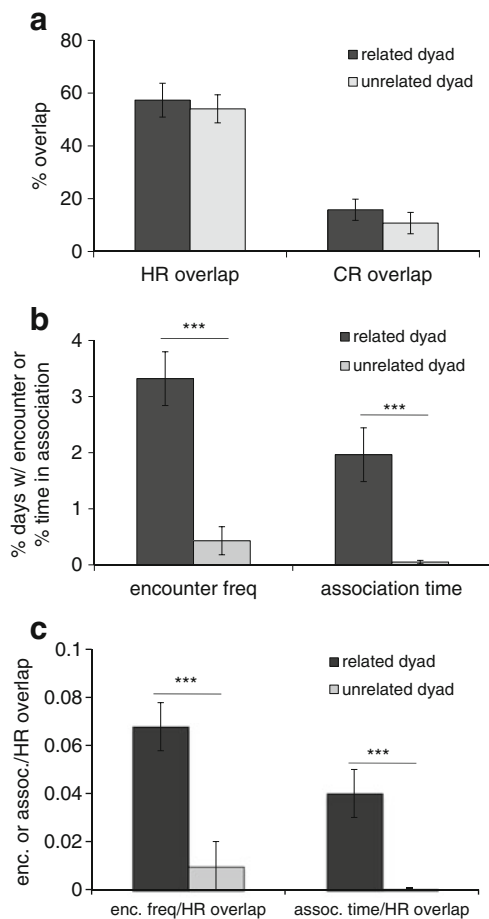
Fig. 2 Comparison between maternally related females dyads and unrelated dyads in (a) their home range (95% use area) and core range overlap (50% use area), (b) encounter frequency (% of days with an encounter per dyad) and percentage of total focal time spent in association, and (c) encounter frequency and association overlap controlled for home range overlap. Unrelated dyads were only included if their home range overlap was at least 32%, the lowest overlap among related females. Significant differences between adjacent columns are indicated with ***P<0.0001

Social interactions during associations Agonism. Even if we restrict analyses to the relatively short associations (<3 h) observed among unrelated females, associations among non-kin dyads differed from those among kin-dyads (Fig. 3), with a higher frequency of severe agonistic interactions (i.e., with active chase and or physical fight including hitting or biting: in 8 out of 37 associations vs. 5 out of 98 Fisher exact P=0.008). In addition, agonistic interactions among non-relatives always (8/8) led to immediate termination of the association and only in 2/5 of the cases among related dyads. (All severe agonism among relatives was between the same two half-sisters).

Feeding tolerance. During associations females hardly ever engaged in positive social activities (only once brief grooming in a mother–adult daughter dyad), but sometimes showed tolerance by feeding within 10 m of each other in the same
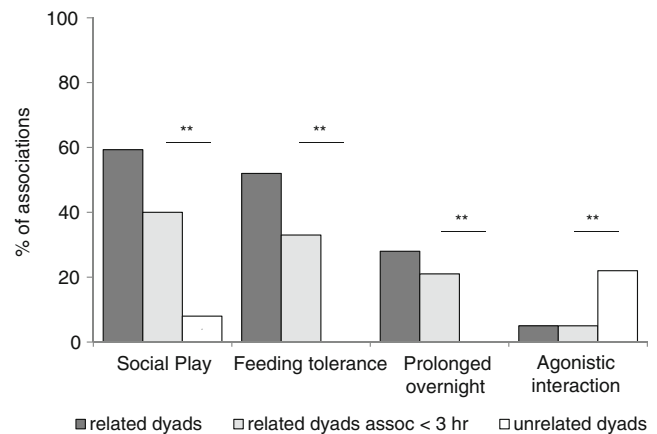

Fig. 3 Comparison of social behavior during associations between related females, associations between related females lasting <3 h and associations between unrelated females (all lasting <3 h): the percentage of female–female associations with at least some social play among immatures, feeding tolerance among females (i.e., both feeding within 10 m), prolongation of the association overnight, agonistic interaction between the females. Significant differences between adjacent columns are indicated with **P<0.001

food patch. Such "feeding tolerance" was never seen during associations of non-related dyads, but in 32 of 98 (32.7%) of those of maternal relatives (χ^2=14.08; P<0.001; Fig. 3).

Social play. Despite the females' lack of affiliative interactions during most associations, their respective offspring frequently engaged in social play (mostly arboreal play-wrestling). Related mothers rarely terminated, and sometimes even actively enabled play among peers while protecting very young infants, and mothers, especially of infants <3 year of age, sometimes even actively participated in such play. However, mothers intervened and effectively prevented contact among non-kin peers on several occasions, by either retrieving their own offspring or chasing away the other immature if it was accompanied by its mother. As a result, social play between unweaned immatures was only seen (briefly) during 3 (of 37) associations between non-related female dyads, whereas play was observed during 40 (of 98) of the associations between relatives (χ^2=11.77; P<0.001; comparing only associations lasting <3 h to decrease bias in favor of related dyads; Fig. 3). Nevertheless, when weaned immatures ranging independently from their own mother (>50 m away) visited a non-related mother–offspring pair, they were "allowed" to play with dependent offspring (observed during at least 6 different focal follows), even for a prolonged period (average play duration 60 min).

In summary, encounters between unrelated females rarely resulted in long-lasting association, and never included simultaneous feeding in the same food patch. Agonistic termination of such associations was also more likely than of associations among related females. In contrast, the close kin associations are characterized by tolerance during feeding and tolerance and accommodation of play interactions among their offspring.

Female cluster size and infant playing time

The Tuanan study area included the ranges of one matrilineal kin-group with a mother and her three adult daughters and another mother–adult daughter dyad ranging at the edge of the study area (insufficient data on one of these two females). In addition, data were collected on three adult females ranging mostly (but not completely) in the study area, and for these females no living adult maternal relatives were known. Even though these females may have had relatives living outside the study area, those were never encountered during follows. Thus in the study area, immatures had access to kin clusters of different sizes, and therefore they were likely to grow up with different opportunities for social interactions with peers. Indeed, in this study females and their offspring of the larger kin cluster with four adult females spent more time in total in association with other adult females than those with only one or no known adult maternal relatives (average $6.15\pm3.07\%$ vs. $0.34\pm0.08\%$; Mann–Whitney $U=0$, $N_1=4$, $N_2=4$, $P<0.05$ two-tailed; whereas large and small kin cluster females did not differ in % time in association with unrelated females: $U=10$, $N_1=4$, $N_2=4$, NS). Even though this comparison is based on only one large maternal cluster *vs.* several females from small clusters, these data suggest a matriline size effect on social opportunities for maturing offspring.

The time difference in time spent in association with peers (and their mothers) was reflected in the time budgets for 1–5-year-old-dependent immatures, indicating that immatures growing up in the large kin cluster consistently spent more time in social play than immatures growing up in a small kin cluster (average $1.18\pm0.92\%$, $N=11$ yearly values of at least 150 h of focal data for the large cluster vs. $0.06\pm0.06\%$, $N=5$ for the small; Mann–Whitney $U=4$, $N_1=11$, $N_2=5$, $P<0.01$ two-tailed). Despite the small sample sizes, these data strongly suggest that maternal cluster size affects the amount of social play with peers an immature can achieve.

Discussion

Dispersal and philopatry

We used observational and genetic data from a single study area to investigate the relatedness patterns among the resident adults in a non-gregarious great ape. Genetic analyses focused on close maternal relatedness, since female ranges were very stable and the maternal range is therefore the best predictor of an adult's natal range. The combination of ranging data and the genealogical reconstruction of all adults sighted in the study area indicated that whereas 4 parous (plus at least 2 nulliparous) females lived in

overlapping ranges with their surviving mother, we found only one young male being maternally related to a known female at the periphery of the study area. Thus, our results strongly suggested female philopatry (sensu Waser and Jones 1983) and male dispersal and are therefore consistent with other recent genetic studies (Arora et al. 2010; Morrogh-Bernard et al. 2011; Nater et al. 2011).

From the Tuanan results, we could also estimate the age at which males disperse from their natal area. The 1 male with a female relative in the study area was still young (estimated <15 years old) and never seen in the same area or in association with his mother. At least 4 unflanged males had a "nonlocal haplotype," e.g., different from all of the sampled parous females (Arora et al. unpublished data). These 4 males were frequently present (10–50% of the months) in the study area, indicating they had moved away from their natal area while they were still unflanged. We therefore conclude that males tend to disperse from their natal range as adolescents. Morrogh-Bernard et al. (2011) concluded that males do not disperse before growing flanges. However, their conclusion was based on a small sample, and is not easily reconciled with the fact that unflanged males are known to sire offspring (Utami et al. 2002; Goossens et al. 2006). We therefore suspect that our conclusion holds more generally.

Recent genetic analyses of the Y-chromosome suggest that males may disperse remarkably long distances away from their natal areas (Nietlisbach 2009). However, here we found that male orangutans not only disperse spatially (away from natal area), they also do so socially (away from known relatives; cf. Isbell and Van Vuren 1996). First, among the males in the study area, no close maternal male kin could be identified. Second, male–male associations, even among unflanged males, were of significantly shorter duration than associations between related females, and no consistent associates could be detected, suggesting the absence of the social bonds expected if there was parallel dispersal (see also Supplementary Fig. 1). Females, in contrast, appear to stay in the familiar area and also near their familiar female relatives, although we would need to sample a larger area to assess whether all females manage to do so. Overall, therefore, the genetic results strongly support behavioral evidence for female philopatry and continuing association with relatives in Bornean orangutans, and the opposite pattern in males.

Female relationships and the social benefits of philopatry

It is possible that maturing individuals with a greater number of tolerant role models would have acquired a larger number of learned skills by the time they are adult. Although infants peer largely toward the activities of their own mothers they also do so occasionally with other cluster

members (Jaeggi et al. 2010), but never with females of other clusters. However, given the small sample sizes, the fitness benefit is hard to quantify. Future work will attempt to estimate these benefits.

In this study, the most conspicuous behavior during associations was social play. Even though related female dyads seemed to choose to approach and spend time in proximity, adults tended to watch each other initially and only gradually approach to within 5 m. Females' dependent offspring, however, tended to approach each other quickly and start social play within the first minutes of the start of the association. Successful maternal intervention, by chasing the other immature or retrieving her own offspring, was seen on several occasions when unrelated females were in brief association and their infants approached each other. The few observations of social play between unrelated immatures almost all happened in the absence (>50 m away) of 1 of the mothers, or when 1 of the mothers was distracted by a consortship with a male. Lack of maternal proximity and attention only occurred for immatures of at least 5 years old. This pattern suggests that the lack of play among peers born in different maternal clusters is due to the mothers' reluctance to allow their offspring to interact and not to a lack of interest on the part of the immatures.

Opportunities for social play among peers are rare for this sample of wild Bornean orangutans. Even though some mothers occasionally actively engaged in social play with their young offspring, they certainly did not do this every day. An older sibling, if present, is at least 7 years older and thus much larger and, most importantly, no longer in frequent association by the time the infant is 2–3 years old and ready to move more than a few meters away from the mother (van Noordwijk et al. 2009). However, when related mother–offspring pairs were in association, immatures frequently played and seemed to forego not only solitary play (which accounts for 20–50% of a 1–4-year-olds' average time budget), but also reduced their time feeding and resting (sometimes by >10%; unpublished data). Even before weaning, social play in this population did not exceed 4% of the average yearly time budget, whereas it drops to less than 1% after weaning (unpublished data). Nevertheless, immatures seem to take advantage of every opportunity they can get to engage in social play with peers, whereas during their associations, adult females rarely engage in social exchanges (such as grooming or food sharing) and merely tolerate proximity (or not). Thus association among parous females seems to be in the interest of the offspring more than of the mothers themselves.

Why would it be beneficial for mothers to provide opportunities for social interactions with peers? Social play, especially during development, is seen in all primates and indeed most mammals and birds as well as other vertebrates (Fagen 1981; Graham and Burghardt 2010). The major

functions of play are thought to be facilitation of motor development (e.g., Byers and Walker 1995; Nunes et al. 2004), and brain development (e.g., Lewis and Barton 2006; Pellis 2010), and preparing the individual to respond to unexpected events (Špinka et al. 2001). Yet, the fitness consequences of a lack of social play under natural conditions are still little known and hard to measure, although one study on Alaskan brown bears, (Fagen and Fagen 2009) reported a positive correlation between social play and survival to independence in Alaskan brown bears, irrespective of food availability and maternal condition. However, despite several plausible hypotheses about the benefits of social play, it remains to be determined whether the difference we found in this study between a little bit of play (on average ca. 1 h per week) for the "large-kin-cluster" immatures and virtually nothing (a few minutes per week) for the "small-kin cluster" immatures, could affect the orangutan immatures' (social) development and, therefore, be biologically meaningful.

Assuming that social play is important for the development of their offspring, why would mothers not tolerate play among non-relatives, or only when the other mother is absent? When an independent immature "visits" a mother–offspring pair, the mother, being larger, can easily intervene in the social interaction whenever her offspring signals distress or is risking injury by falling out of the trees. However, if another adult female is also present, she may be less able to quickly rescue her offspring. This might explain why females tend to tolerate the offspring's interactions with well-known maternal relatives, who benefit to some extant from the well-being of both immatures, but are wary or antagonistic towards unrelated females with whom they do not share a common interest. Another explanation may be that it is generally costly for females to spend time in association (potential scramble competition) and when they do this for social reasons (or their offspring's social benefit) prefer a familiar association partner. Familiar partners are likely to impose the lowest physiological cost (lowest stress response) by being predictable and having some shared interest.

Among East African chimpanzee females, who can be almost as non-gregarious as orangutans, severe female aggression has been documented, resulting in the death of a competitor's offspring (Goodall 1986; Pusey et al. 1997; Townsend et al. 2007). Even though orangutans have never been seen to form coalitions in the wild, as in the documented cases of female infanticide in chimpanzees, females have been seen to fight (including biting) with each other on rare occasions. Thus the potential for serious harm to unprotected young immatures is clearly present. In general, mistrust between unrelated females is expected because of the potential harm competing females could do to each other's offspring (cf. offspring-defense hypothesis: Wolff

and Peterson 1998), whereas tolerance is found to be higher among related neighbors (Waser and Jones 1983; Kitchen et al. 2005). It is noteworthy that orangutan females without offspring (nulliparous and females with only older weaned offspring) were more likely to range over a larger area, but retreated into their established range after the birth of their next offspring (van Woerden and Pettersson 2007, and un-published data). A likely benefit of the more restricted ranging of mothers with young offspring may be that within their smaller range the risk of encounters with strangers is smaller. We have shown here that females respond very differently to encounters with maternally related females vs. maternally not related females. This suggest a potential risk posed by unrelated females, even though this may be hard to document.

Dispersal and female relationships in the great ape lineage

This study showed that females of the least gregarious extant great ape actually do maintain social relationships with their philopatric maternal female kin and so seem to enable the development of social bonds among their off-spring. In this respect, orangutans are very similar to many other primates living in matrilineal groups, but different from the African great apes which have a tendency for female dispersal with limited opportunity for female bond-ing. Thus, these results illustrate the variability in philopat-ric tendencies among all great apes from strongly male-biased to strongly female-biased dispersal.

Perhaps more importantly, the results underscore the fact that orangutan females, in spite of their philopatric tendency, may occasionally live without any nearby adult female relatives. However, the long-term fitness consequences for their offspring remain to be examined. Among the other great apes, females seem to be even more flexible. For example, although chimpanzee females are sometimes able to stay in their natal community and then maintain matrilin-eal bonds (Goodall 1986; Pusey et al. 1997), they can also form supportive dyadic relationships with particular unre-lated females after dispersal (Wakefield 2008; Langergraber et al. 2009; Wild 2010). Bonobo females also form close bonds with unrelated females (Hashimoto et al. 1996) and gorilla females are sometimes able to maintain social bonds with relatives as well as with unrelated females (Watts 1994; Bradley et al. 2007). This ability to form and maintain bonds has freed females from the necessity to be strictly philopatric.

Similar flexibility and independence from philopatry for the formation of intrasexual bonds is also seen among human females. Hill et al. (2011) recently showed that among hunter-gatherers, an individual's or even a female–male pair's site of residence may vary throughout the life-time. This unusually flexible pattern of dispersal enables a young mother to live near maternal kin and receive their support when she most needs it, but also enables males to co-reside with male kin and form coalitions at other times in their life. As data on great apes accumulate, a similar flex-ibility in philopatry and dispersal is becoming apparent.

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