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Master Thesis

Male affiliative relationships in Sumatran orang-utans – Why do unflanged males form temporary associations?



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Male associations in Sumatran orangutans – Why do unflanged males form temporary groups?

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The bimaturism of male orangutans leads to two adult morphs that differ in behaviour and physical appearance. Unflanged males can arrest the development of secondary sexual characteristics that define fully developed flanged males for many years. While flanged males produce long-calls to advertise their presence, unflanged males are more mobile and move around larger areas to find receptive females. Genetic studies have confirmed that both male morphs can sire offspring. Of the two orangutan species, more pronounced gregariousness is observed in the Sumatran orangutan and it has been suggested that this difference derives from the higher habitat productivity on this island. Besides females, unflanged males also associate more frequently. These temporary associations have been described as travel bands but the benefits remain unclear. To better explain these associations, we analysed detailed focal animal data from 41 individually known and several unidentified unflanged males (1652h of observations) collected over 10 years at Suaq Balimbing (Aceh Selatan, Sumatra). We used this data set to investigate the composition and duration of unflanged male associations for the first time in detail. To assess costs of associations we looked at daily feeding proportions and time unflanged males spent with females or other unflanged males. We measured daily feeding proportions in different association types and we compared the time unflanged males spent with females or other unflanged males during single-male and multi-male associations. There was no evidence for energetic costs for unflanged males. Furthermore, we analysed behavioural interactions observed during unflanged male associations with all three sex/age classes (adult female, unflanged male, flanged male). Unflanged males were more tolerant and showed more affiliative behaviour in association with females or other unflanged males, compared to associations with flanged males. The high fruit availability at this study site, and for this reason the low cost of association, in combination with beneficial opportunities for social learning, might have led to stronger affiliative relationships between unflanged males than previously expected.

Introduction

Affiliative social relationships in mammals have been studied intensely over the last decades (reviewed by Clutton-Brock & Janson, 2012). Social systems stretch along a "continuum of cohesiveness" ranging from a solitary lifestyle up to stable social bonds (Shultz & Dunbar, 2010). A social relationship can be defined as the combination of interactions between two individuals (Hinde, 1976; Wrangham, 1980). A relationship can be seen as a potential investment that may lead to benefits in the future (Kummer, 1978). While some authors have treated the terms social relationship and social bond synonymously (e.g. Silk, 2002), others define social bonds as a special kind of reoccurring and long-lasting social relationship between two individuals (e.g. Ostner & Schülke, 2014). However, language to describe and classify social systems and the affiliative processes that shape them is still missing (Shultz & Dunbar, 2010).

Most studies on affiliative social relationships have focused on relationships between females, since in most group living species females are more related to each other than males, due to females being the philopatric sex (Cote et al., 2010; Gros et al., 2008; Ronce et al., 2000). Only over the last decade have studies looked closer into affiliative relationships between males. Tolerance and affiliative behaviour between groups of males is less expected because of the competition for access to fertile females (van Schaik & van Hooff, 1994). Nevertheless, we observe affiliative and cooperative social interactions between males in fish (Bender et al., 2006), birds (Emery et al., 2007) and mammals (e.g. bats: Safi & Kerth, 2007; otters: Blundell et al., 2004; racoons: Gehrt et al., 2008; dolphins: Connor & Krützen, 2015; primates: Bercovitch, 1988; Bissonnette et al., 2011; Noë & Sluijter, 1995; Ostner & Schülke, 2014). Males may increase their survival probability or benefit from reproductive advantages by associating with other males (Ostner & Schülke, 2014; van Schaik & van Hooff, 1994). The main proposed mechanisms explaining male bonds are kin selection, reciprocal altruism, and mutualism (Clutton-Brock, 2009; Hamilton, 1964; Trivers, 1971; van Schaik & van Hooff, 1994).

Males may incur fitness benefits if they cooperate in the mating context. As shown by Bissonnette et al (2011), lower ranking male Barbary macaques gain higher mating success through the formation of male-male coalitions. However, in most mammals, only one male

can successfully fertilize a female during ovulation. The most common explanation is indirect fitness benefits through kin-selection (Hamilton, 1964; van Schaik, 1996). Cooperating males can thereby gain indirect fitness benefits by helping close kin monopolize fertile females (Mitani et al., 2000; Watts, 1998). However, cooperative males are not always related to each other (Patzelt et al., 2014; Schülke et al., 2010), making the alternative mechanism, reciprocal altruism, a more likely explanation for some species. According to this theory, males involved in such cooperative male-male behaviour without achieving copulations might have delayed fitness benefits, if they are able to sire offspring at a later time (manakins: DuVal, 2007; chimpanzees: Gilby et al., 2013).

The potential benefits of male affiliative relationships are not restricted to the context of reproductive fitness. Males may gain mutual protection from predators when living in bigger groups with multiple males or even live in bachelor groups when unable to join a bisexual group (Mohnot et al., 1995; Stanford, 1998; van Schaik & Hörstermann, 1994; Waterman, 1997). Additionally, males may benefit by gaining access to a bigger territory through cooperation (Langergraber et al., 2007; Mitani et al., 2010) or by sharing ecological knowledge about the area (Safi & Kerth, 2007; van Schaik et al., 2016). While social systems with stable social bonds have been described (e.g. Berghänel et al., 2011; Kubenova et al., 2017), lower scale cohesiveness lacks examples and definition. Here, we propose temporal associations of unflanged male orangutans as an example for social relationships in unstable aggregations.

Orangutans live semi-solitarily in large overlapping home ranges. Males are the dispersing sex (Nater et al., 2011), while females are philopatric and establish their home ranges close to their mothers (van Noordwijk et al., 2012). Because of the higher forest productivity (Husson et al., 2009; Wich et al., 2011), Sumatran orangutan populations *(Pongo abelii)* exhibit higher densities than Bornean populations *(P. pygmaeus*). Although males and females largely range alone, they do aggregate in times of high fruit abundance and can travel together in so called "bands" for several days (Atmoko et al., 2008; Singleton et al., 2009; Sugardjito et al., 1987; van Schaik, 1999). Both forms of associations, active travel bands and passive feeding aggregations, show different sex/age class compositions (Rijksen, 1978; Setia et al., 2009).

Male orangutans show a distinct form of bimaturism with two male morphs: flanged and unflanged. Unflanged males can develop into flanged males (Dunkel et al., 2013; Maggioncalda et al., 2002; Marty et al., 2015), defined by the growth of secondary sexual characteristics (laryngeal sack, cheek pads, increased body size). This change is irreversible.

Unflanged males have been reported to arrest development for over 20 years (Dunkel et al., 2013). The lack of secondary development has led researchers to classify unflanged males as immature or subadult males in earlier studies (Schürmann & van Hooff, 1986; Sugardjito et al., 1987). However, both male morphs have been reported to sire offspring (Banes et al., 2015; Goossens et al., 2006; Lenzi, 2014; Maggioncalda et al., 2002; Tajima et al., 2018). The two morphs show alternative reproductive tactics (Delgado & van Schaik, 2000; Dunkel et al., 2013; Galdikas, 1985; Knott, 2009; Spillmann et al, 2010&2017; Utami & van Hooff, 2004). Flanged males produce long-calls to attract females and follow a "sitting-calling-waiting" strategy. Conversely, unflanged males are known to roam the area actively searching for females. This has been referred to as the "going-searching-finding" strategy. The latter strategy could be interpreted as a "making the best out of a bad job" strategy, since females prefer flanged over unflanged males (Spillmann et al., 2010, 2017; Utami & van Hoof 2004, 2009).

Unflanged males are the predominant morph found in Sumatra since arrested development is more pronounced in this orangutan species (Dunkel et al., 2013). Additionally, within the Sumatran populations, unflanged males have been reported to be more gregarious and are commonly observed in travel bands with differing sex/age class combinations (Sugardjito et al., 1987; Utami et al., 2008; Utami, 2002). While the associations of unflanged males have been described previously (Fox, 2001; Galdikas, 1985; Utami et al., 2008; van Schaik, 1996; van Schaik, 1999) quantitative data is still missing.

In this study, we present data of unflanged male associations including interactions between males and females. We quantified occurrence and composition of unflanged male associations and social interactions (feeding tolerance, social play, social watch, peering and agonistic interactions). In order to be able to explain the function of these associations, we investigated the costs and benefits for unflanged male's sociality and tolerance.

We predict that males experience low costs while in an association because of high fruit availability. We expected the daily feeding proportions of unflanged males in associations to be unaffected. However, costs for males might not only be in the form of access to food, but due to male-male competition for access to females. We predict that the presence of another male would negatively influence an unflanged male's daily association rate with females as well as its distance to a female. We assume that the benefits of association in male orangutans are mainly in a context of socialization or mating (van Schaik, 1999), since predation

avoidance in a large bodied, arboreal and solitary living organism is unlikely. Rather, we expect social behaviours that could lead to social knowledge transfer or access to females, to be frequent in unflanged male associations.

Methods

Study site and study subjects

Data was collected in the Suaq Balimbing research area (3˚42'N, 97˚26'E, Aceh Selatan, Indonesia). At this research station long-term behavioural data has been collected by field assistants and researchers since 2007. For this study we analysed all unflanged male focal data from April 2007 to July 2018. During this study period, we followed 41 different individually known and some unidentified unflanged males on 260 days (more than 1652 observation hours). Unflanged males can be differentiated from flanged males by the lack of secondary sexual characteristics especially the missing flanges and smaller body size. Adolescent males were not included in the data since they are not yet sexually mature. Males are defined as unflanged males when they disperse into a new area. We distinguished between adolescent and unflanged males based on our knowledge of the individuals as well as body size differences. We took pictures of each individual present during a follow and later identify individuals using our picture data base. Multiple observers have identified each individual in our data set to limit observer errors. However, because we are not comparing data on an individual basis, we also included unidentified individuals, as long as their sex/age classes was known.

Data collection

Monthly phenology scans on two main transects of the study site were conducted to calculate a fruit availability based on the presence of flowers, fruits and young leaves. Behavioural data on unflanged males was collected during focal follows using the standardized protocol (https://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html). The activity of the focal animal and its proximity to other individuals in association was noted at 2-min intervals (later also referred to as bouts). Associations include all individuals within 50m distance from the focal animal. Additionally, more detailed all-occurrence social interactions data between the focal unflanged male and associate was recorded ad libitum (Table 1).

For this study we focused on dyadic interactions (N=210, 116 with adult females, 23 with flanged males and 71 with other unflanged males) which we observed during 132 focal

unflanged male follows (over 1000h of dyadic associations). We only considered adult individuals as potential associate (we excluded interactions with male and female adolescents and all dependent offspring). Based on the composition of associations we distinguished between four types of association (Table 2).

Table 1. Definitions of social behaviours observed. Behaviours from the standard ethogram. We consider feeding tolerance, peering and social play as affiliative interactions since tolerance of both involved individuals is required.

Behaviour	**Definition**
Feeding tolerance (affiliative)	Two or more individuals feed in the same food patch within 10m and on the same item
Social play (affiliative)	Interaction with no apparent or immediate purpose in non-aggressive context where at least two individuals are involved
Social watch	Looking at or in the direction of another individual or its noise and vocalizations, independent on distance for at least 5s
Peering (affiliative)	Close observation of an action of another individual for at least 5s and within 5m
Agonistic interactions	Includes chasing and/or displacing another individual from food patch or copulation

Table 2. Definitions of types of association

Type of association	Definition
Alone	No other individual present within 50m distance of focal
Male with Female	At least one adult female, but no other adult male present within 50m distance of focal
Multi-Male	At least one other adult male, but no adult female present within 50m distance of focal
Multi-Male with Female	At least one adult female and one other adult male present within 50m distance of focal

Data analysis

We calculated daily feeding proportions of unflanged males with focal activity data by dividing the number of bouts per day spent feeding by total number of bouts observed during a day. For this analysis we only used full day (nest to nest) focal follows (N=47). We compared daily feeding proportions of unflanged males in relation to association type observed during the same day. Here we treated association types according to what sex/age classes were present during the whole day.

Peering, social play, social watch and agonistic behaviours were coded as a binary variable indicating presence or absence of the respective behaviour during a follow day for each specific dyad. Feeding tolerance was measured in 2-min bouts obtained from the focal activity data.

We measured the association rate of unflanged males with females by adding all intervals of a follow period were at least one female was present and divided it by the duration of the focal follow. We compared male with female follow days and multi-male with female follow days. Furthermore, we calculated the proximity rate to females using the 2-min interval proximity data from the focal activity. We calculated the close proximity rate by dividing the

sum of bouts spent within 10m by the total number of association bouts for each specific male-female dyad (N=116).

To investigate the relationship between males in relation to association type we measured the proximity rate to other males in the same way as we did for the proximity rate to females (N=92). Additionally, we calculated the feeding tolerance rate by dividing the total bouts spent within 10m during a day with the total bouts spent in feeding tolerance during a day.

All analyses were conducted using R (R Development Core Team, 2013). To investigate the effects association type and class of dyadic partner the Wilcoxon signed rank test or a Kruskal-Wallis test by ranks (to compare over multiple compositions) was carried out using the ggpubr package (Kassambara, 2017).

We conducted multiple measures form the same individual in the data, this might lead to pseudo replications. A more thorough analysis is planned in which we will analyse our data with generalized linear models. Furthermore, we could not include more detailed rates of social behaviours because we do not have enough data. We did not include copulations into the data set because we did not have the time of the interaction in our data set and hence association types would be missing.

Results

Composition and social behaviour during association

Overall, we observed unflanged males in association on 149 of the 260 follow days (57.3%). Associations lasted up to six days, on average they lasted about 3.287h ± 4.321 (mean ± sd). Unflanged males spent about half of their focal follow time alone (average daily proportion (ADP) = 53.7%). When they were in association with other individuals, it was mostly one male with one or multiple females (ADP = 28.9%), but we did observe multi-male with female (ADP = 9.5%) as well as male only associations (ADP = 7.9%). In 21 out of the 29 occurrences of multi-male-female associations, only other unflanged males and no flanged males were present. On average unflanged males spent 0.37h (± 1.67h) with flanged, 0.9h (± 1.96h) with unflanged males and 2.91h (± 2.1h) with females during a day with association (6.97h ± 3.9h), this could be during all types of associations.

During associations we frequently observed affiliative and tolerant social behaviour (Table 3). Most common interactions were feeding tolerance, peering and social watching. Most of these interactions were observed between unflanged males or with a female. Interactions with flanged males where mostly agonistic. However, agonistic behaviour also occurred between focal unflanged males and females in 16 occasions. Five times a focal unflanged displaced a female from a food patch and at least one time an unflanged male mate guarded a female, holding her arm and preventing her to move away. We did see a female displacing an unflanged male from a food patch as well. On six occasions we observed agonistic behaviour between unflanged males. Two of these involved an unflanged male displacing another male from a copulation with a female. We did not observe any injuries deriving from agonistic behaviours and we did not observe physical contact in this context between males.

Table 3. Number of social behaviours observed during unflanged male focal follows. In the last row we present the total numbers of dyadic associations with the three sex/age classes. We also show the percentage of dyads a behaviour was observed in.

Behaviour	Females	Flanged males	Unflanged males
Feeding tolerance	49 (42.2%)	0	23 (32.4%)
Social play	4 (3.4%)	0	4 (5.6%)
Social watch	27 (23.3%)	7 (30.4%)	11 (15.5%)
Peering	27 (23.3%)	0	5 (7%)
Agonistic	16 (13.7%)	11 (47.8%)	6 (8.5%)
Total	116	23	71

Costs of association

Based on full day focal follow data, the daily feeding proportion did not significantly change when unflanged males were in association with other individuals, independent of the type of association (Kruskal, p=0.66, p.adj. = 0.66;Fig. 1). On average, unflanged males spent more than half of the day (from morning nest until evening nest) feeding (average daily feeding proportion = 0.538). We found no correlation between feeding time and fruit availability (Pearson, p=0.282, t=1.093). However, the sample size was very small (N = 40). Unflanged males' feeding proportion was also not affected by association types during focal days (Fig. 1).

Fruit availability had no significant influence on the observed group size (Kruskal-Wallis, p=0.428, N = 88, group levels were the group size of a follow day, ranging from one until nine). We predicted that the presence of other males might negatively impact the access to a female. Contradicting our expectations, we found that unflanged males spent a significantly higher proportion of time within 10m to a female in a multi-male association compared to days when they are the only male in proximity of a female (Wilcoxon, p=0.032, p.adj.=0.028; Fig. 3).

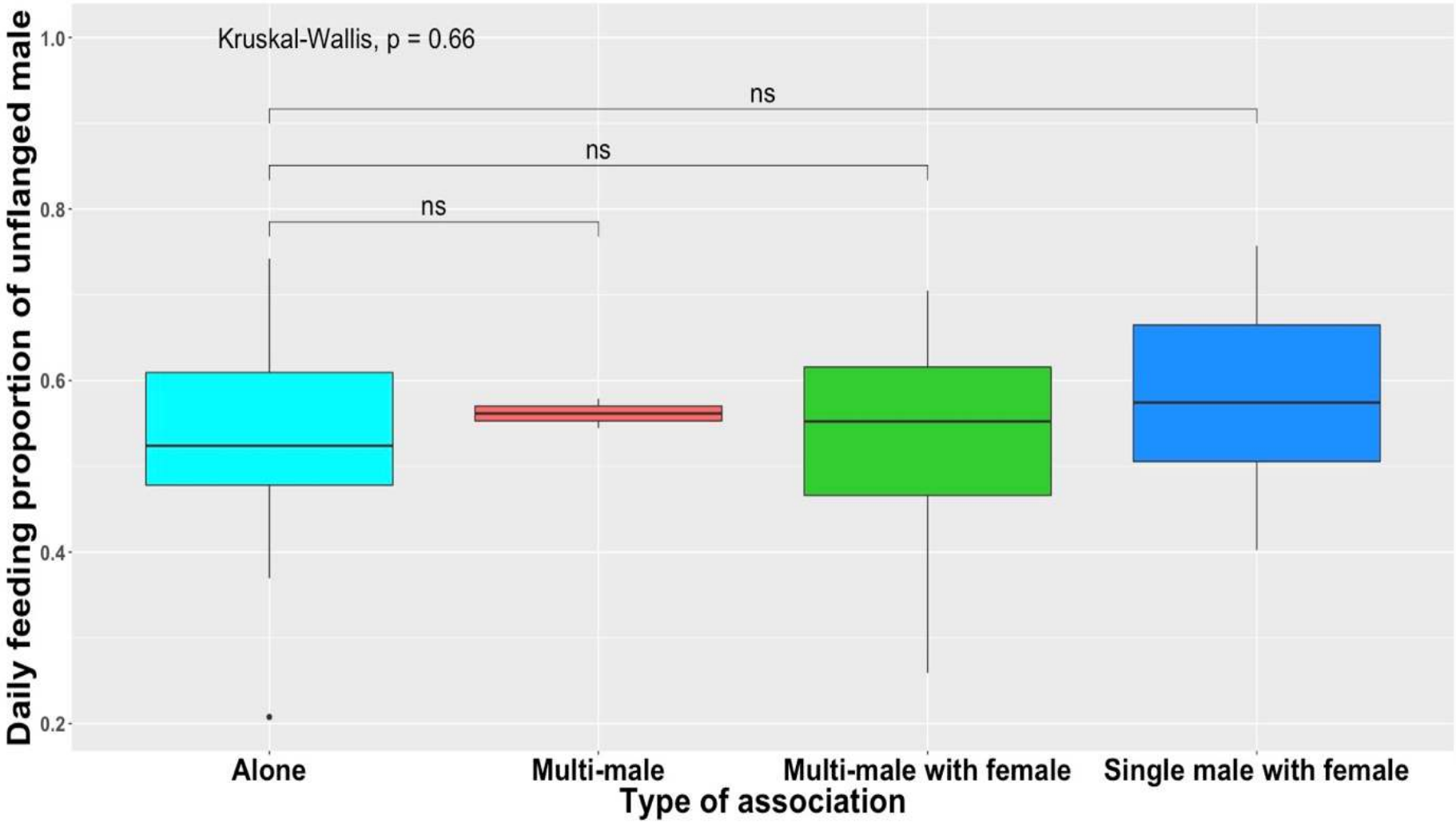


Figure 1. Proportion of feeding time of unflanged males during full day follows when in association and alone. Kruskal Wallis, p=0.659 , p.adj.=0.66; Pairwise group comparision using Wilcoxon between: Alone and Single male with female, p= 0.234, p.adj.=1, Alone and Multi-Male with female, p=0.901, p.adj.=1, Alone and Mulit-male, p=0.532, p.adj.=1

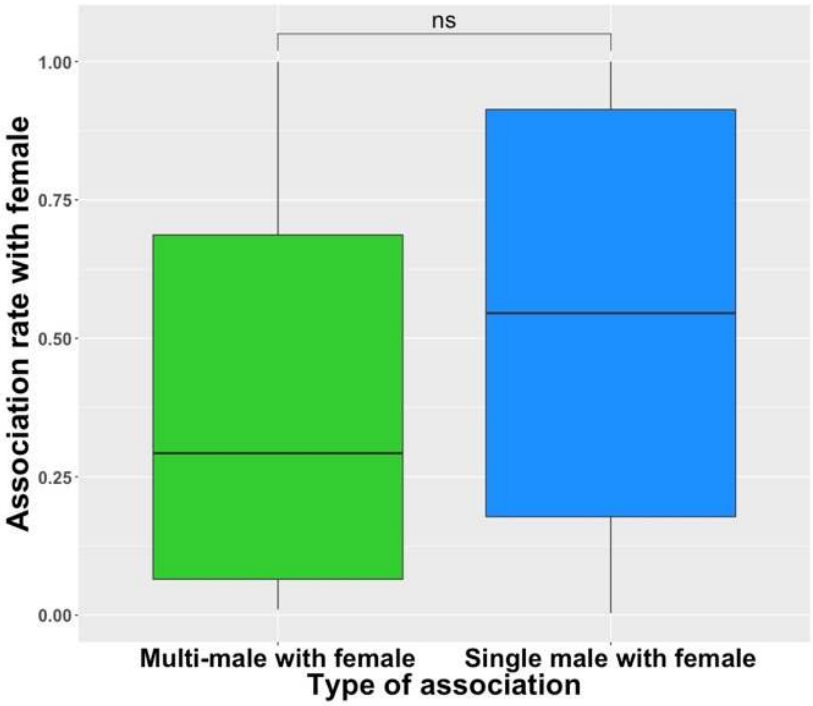


Figure 2. Unflanged male daily association rate with females on focal follow days with single male with female and multi-male with female follows. Pairwise group comparison using Wilcoxon, p=0.077, p.adj.=0.044

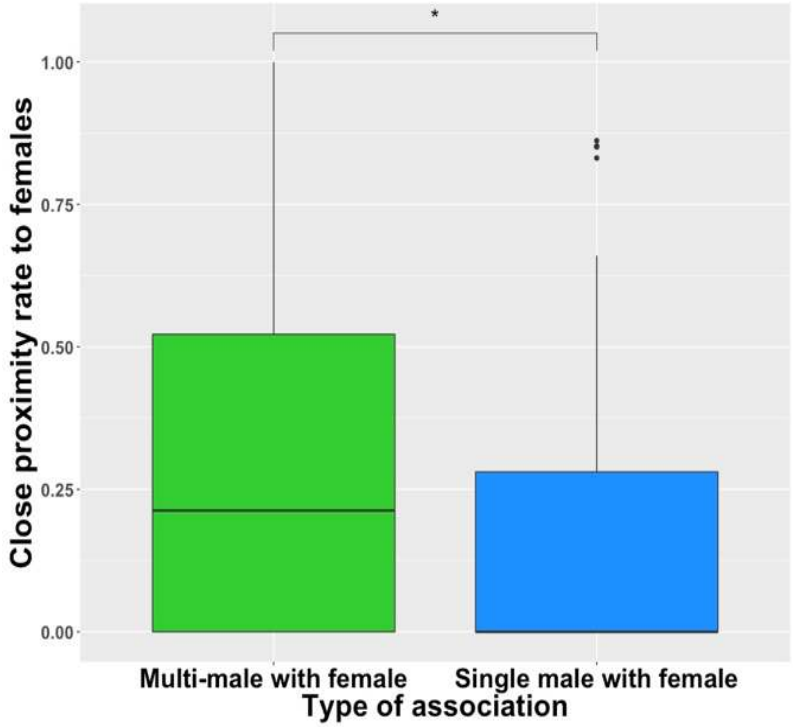


Figure 3. Unflanged male daily close proximity rate to females on days with single and multi-male follows. Pairwise compairison using Wilcoxon: p=0.032, p.adj.=0.032

Male-male relationship

Unflanged males spent significantly less time within 10 metres of flanged males (6.7% of association time) than with other unflanged males (24.7% of association time; Wilcoxon, $p < 0.001$, p.adj.<0.001) or females (27.4% of association time; Wilcoxon, p<0.001, p.adj.<0.001)(Fig. 4). We observed no feeding tolerance between unflanged and flanged males. However, females showed feeding tolerance with unflanged males on average 15.4% of the bouts they were within 10m. Unflanged males showed feeding tolerance in 10% of the time when they were in close proximity to unflanged males.

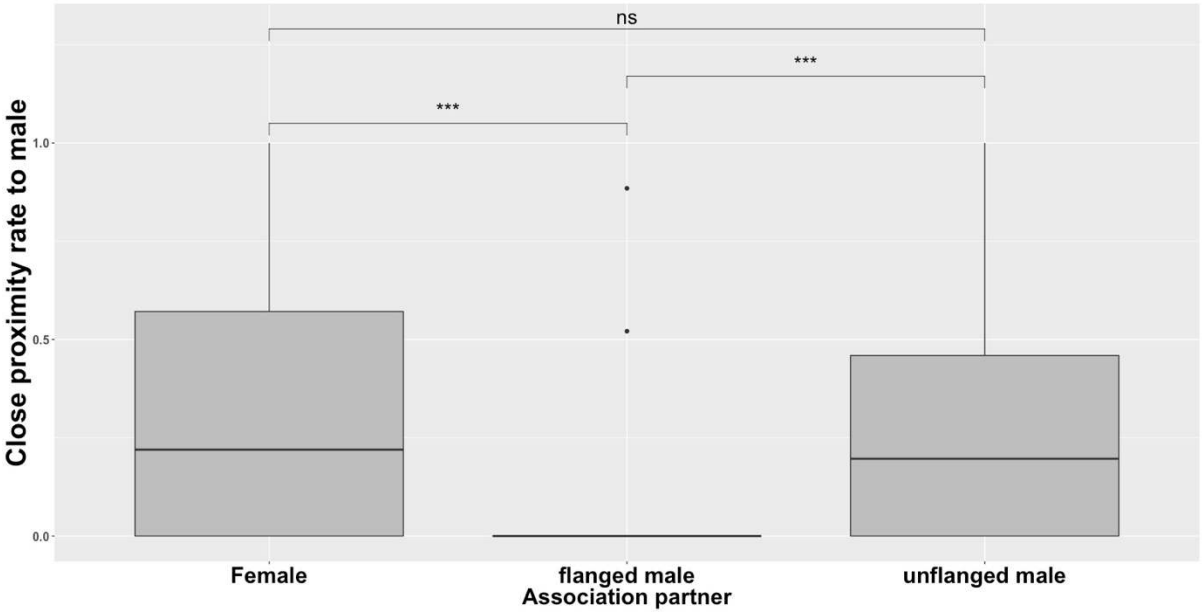


Figure 4. Close proximity rate of focal unflanged males compared between flanged male, unflanged male and female associations partners. Pairwise comparison using Wilcoxon between: unflanged male and flanged male, p<0.001, p.adj.<0.001, unflanged male and female, p=0.558, p.adj.=0.56, flanged male and female association partners, p<0.001, p.adj.<0.001

Discussion

We looked at possible arising costs and benefits of unflanged male associations. We predicted costs to be low because of high fruit availability (Husson et al., 2009; Wich et al., 2011). Since benefits are expected to be mainly social (van Schaik, 1999) unflanged males should associate often and with high rates of affiliative social behaviour.

Unflanged males at Suaq associated frequently with females and other unflanged males. Focal animals were in association almost every second day. The composition of associations varied, but on average unflanged males associated longest with females. We did observe multi-male associations on 12 out of 149 association days. Generally, unflanged males showed a similar rate of affiliative behaviour towards both females and other unflanged males. Affiliative behaviour (like social play) also occurred between unflanged males in these associations when there was a female present. This indicates that unflanged male dyadic interactions may be beneficial if they are (at least at times) preferred over a female dyadic partner. On 75 of the association days, unflanged males were observed in multi-male-with-female groups. This fits previous suggestions that unflanged males follow a "go-and-search" strategy to seek access to females but are tolerant towards other unflanged males (Husson et al., 2009; Utami et al., 2008; Utami & van Hooff, 2009; Wich et al., 2011). However, we had two observations of an unflanged male displacing another unflanged male from a copulation which may show evidence of sexual competition nevertheless existing.

Unflanged males are known to have long day ranges (Galdikas, 1985; Utami & van Hooff, 2009). Our data includes focal follows with non-consecutive days on which males have left the area or we lost sight of the focal animal. This could bias our data since we generally follow focal animals only until 200m outside of our study area. Furthermore, even though focal unflanged male data is present throughout the period of 2007 until 2018, we increased our focus on unflanged males since 2017. About half of our focal follows have been taken in the last two years and this is also the time were we mostly observed multi-male with female associations.

Daily feeding time of unflanged males was not affected by association type. This indicates that unflanged males carry little to no energetic costs when associating with others. This might be related to the high fruit availability of Suaq and may explain why unflanged males follow a more affiliative lifestyle compared to other populations (van Schaik, 1999).

Social peering is a behaviour involved in the process of social learning (Schuppli et al., 2016). While we cannot present data on social learning in unflanged males because we would need to show that unflanged males actually replicate actions they observed and we are missing the data for this, the frequent occurrence of peering behaviour and social watching combined with the low costs of associating strongly suggests that social knowledge is a benefit of being in association with other males or females. Unflanged males were involved in peering interactions on 28 out of 115 days in which they were observed to be in an association. In every unflanged observed male-female dyadic association involving peering, focal unflanged males peered at the female. In half of these dyads females also peered at the unflanged male during the follow. Considering that males are the dispersing sex (Nater et al., 2011), local ecological knowledge as well as novel variants of feeding techniques can be highly beneficial for unflanged males, especially upon arrival. Similar, this might also be beneficial to females and their offspring, since males could act as cultural vectors, carrying novel innovations between populations (Mörchen, 2016). Social information could not only be beneficial in ecological but also in social context. Associations with females provide chances of monitoring the receptive status of females. Female orangutans have concealed ovulation (Knott et al., 2009), hence males might not know the fertility status of females (Fox, 1998; Knott et al., 2010). However, males could estimate the reproductive status of a female based on the size of their offspring (Cadilek, 2009). Additionally, hand raised orangutan males can lack sexual interest in females (personal communication Clemens Becker). Observing male female interactions in the context of sexual behaviour could thus be important for the development of the future sexual behaviour of unexperienced males.

While interactions between unflanged males were mostly tolerant, we did also observe agonistic interactions on 6 of 149 association days. Two of these involved an unflanged male displacing another unflanged male from a female while copulating. There are no records of injuries or any observations of physical fights between unflanged males in our database of over 10 years of data. Nevertheless, the male-male associations may have an influence on the individual fitness of the males if they don't get close to the female and are kept from copulating. However, the unflanged males' close proximity to females actually further increased during associations with other males. Since males do seem to compete over the access to females at least to some degree considering the displacements from copulations, the higher closer proximity might be a sign of mate guarding and the presence of other males

may force them into closer distance to females. Kunz (in prep.) show that males copulate more often in the context of the perceived presence of another male. Although paternity data is scarce and it remains difficult to assess the paternity success, we know that they can sire offspring in the wild (Banes et al., 2015; Goossens et al., 2006; Lenzi, 2014; Maggioncalda et al., 2002; Tajima et al., 2018).

We observed similar rates of affiliative behaviours between unflanged males and females compared to interactions between unflanged males. This lets us suggest a more than merely tolerant relationship between unflanged males since these behaviours involve tolerance from both individuals simultaneously during context of potential feeding competition. The occurrence of peering behaviour could be an indicator that social information transfer between unflanged males takes place. These social affiliative behaviours were also observed in multi-male with female associations. This shows that unflanged males choose to interact with other unflanged males not due to a lack of a better choice, since they peer towards males even if a female is close by.

Social play behaviour was shown to positively impact brain development and behavioural flexibility (Montgomery, 2014). Additionally, play behaviour between males has been suggested to serve as means of assessment of strength or even establishing ranks (Paquette, 1994; Pellis & Pellis, 1996). These benefits could also explain why we observed play behaviour between unflanged in our study in 4 out of 149 association days. Although we do not have the data to test it, a hierarchical structure within the unflanged males may exist. We observed unflanged males displacing other unflanged males but never observed a fight. Assessment of the strength of other males and hence knowing ones position in the hierarchy could take place during unflanged male social play. In addition, play behaviour could also function as physical preparation for a fight.

Schultz and Dunbar (2010) suggested three novel measurements for bondedness: vocal exchanges, monitoring and behavioural synchrony. While we cannot present data on directed vocal exchanges in this study, we will discuss social monitoring and behavioural synchrony to imply indices for possibility for bonding in unflanged males. Orangutans show a variety of vocalisations in the wild (Hardus, 2009), but we could not include vocalization data in our analysis since it is difficult to entangle the direction of calls. We did however analyse data on social watching. This behaviour involves an individual looking in the direction of a conspecific to possibly obtain information about its behaviour or position. Schultz and Dunbar (2010)

argue that monitoring a social partner can be a sign of attentiveness as it would be expected in social bonding. Social watching was a frequently occurring behaviour of focal unflanged males while in association. In the context of looking into the direction of noise emitted possibly from another male, monitoring might be a pure vigilance behaviour to detect competitors (e.g. pata monkeys: McNelis & Boatright-Horowitz, 1998). However, social watching occurred during neutral or affiliative interactions as well (e.g. looking at a female while she is moving to another tree or looking at an unflanged male during social play behaviour). This could be interpreted as attentiveness towards association partners as observed in baboons (Maciej et al., 2013). We also recorded feeding tolerance, a behaviour where a dyad feeds within the same food patch and on the same food type. This could also be interpreted as behavioural or feeding synchrony. At least in ungulates feeding synchrony, defined as adjusting feeding, resting and moving behaviour with members of your group, helps to avoid segregation (Dunbar & Shi, 2008; Ruckstuhl & Kokko, 2002; Ruckstuhl & Neuhaus, 2000). Unflanged males spending time in association with a female could be trying to avoid segregation to prolong the association. Here, the similar size of unflanged males and females due to developmental arrest may involve little costs for males when adapting to the female's behaviour since they have similar energetic needs. A further benefit of synchronic activity has been shown in studies on humans, in which increased endorphin levels and an increase in generous behaviour was found (Cohen et al., 2009; Wiltermuth & Heath, 2009). Through this synchronic activity relationships could gain in strength (see Schino & Aureli, 2009). We find evidence for both social monitoring and behavioural synchrony in unflanged male orangutans associating with females and also with unflanged males. This suggests that unflanged male associations might be more than just tolerant relationships.

Social bonds are reoccurring affiliative interactions between two individuals. Our data confirms the presence of affiliative relationships in unflanged male association, but we cannot show such relationships to be reoccurring between the same individuals. The inclusion of the so far not analysed all occurrence data from additional focal follows, as well as collecting more data in the field could improve our understanding of association patterns between individuals.

Unflanged males showed affiliative behaviour also towards other unflanged males. We did not find evidence for costs involved in associations for Sumatran unflanged male orangutans. However, we find potential social benefits of association. Dyadic relationships showed

frequent affiliative behaviour and we found evidence for two of the three novel measurements proposed by (Shultz & Dunbar, 2010) defining social bonds; behavioural synchrony and social monitoring. Unflanged male associations might be an example for lower scale cohesiveness with temporal aggregations. Keeping costs low and benefiting from opportunities of social learning might be “doing the best out of a bad job”.

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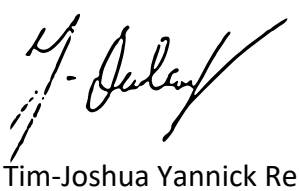
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Statement of Authorship:

I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

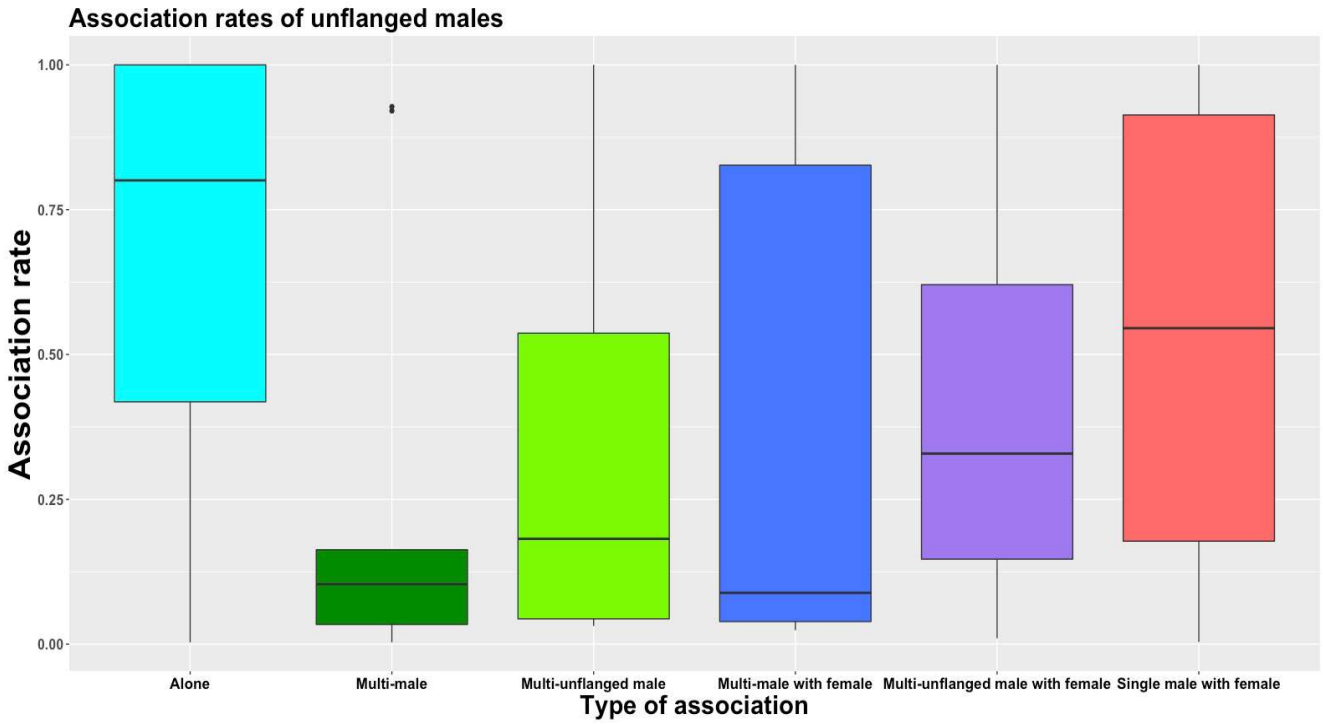
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Tim-Joshua Yannick Reukauf

Appendix

Association rates of unflanged males compared in detailed association types



Supplementary figure 1: Association rates of unflanged males compared over detailed types of associations.

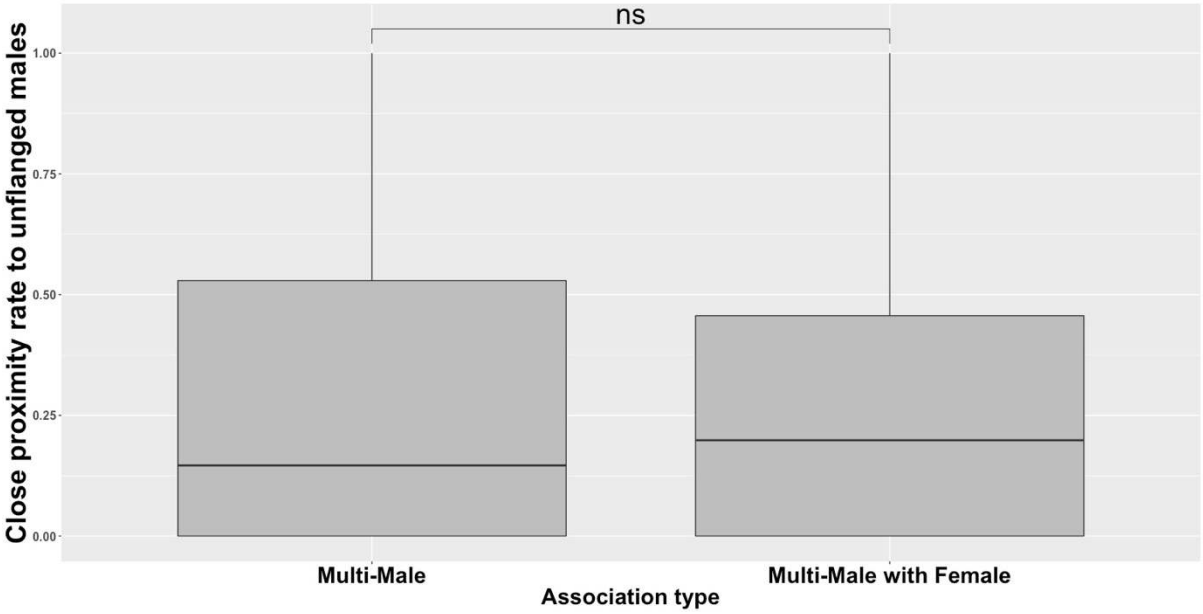
Detailed types of associations were distinguished as follows: alone, multi-male (male only associations with a flanged male present), multi-unflanged male (male only association without a flanged male present), multi-male with female (mixed sex association with at least one flanged male present), multi-unflanged male with female (mixed sex association without a flanged male present), single male with female (focal unflanged male with at least one female). Unflanged males spent more time with other unflanged males or females than they did with flanged males. However, the mere presence of a flanged male did not necessarily shorten the time spent in a multi-male female association.

Daily feeding proportion o unflanged males

.y.	group1	group2	p	p.adj	p.format	p.signif	method
FeedingProportion	Alone	Multi-male	0.532	1.000	0.53	ns	Wilcoxon
FeedingProportion	Alone	Multi-male with female	0.901	1.000	0.90	ns	Wilcoxon
FeedingProportion	Alone	Single male with female	0.234	1.000	0.23	ns	Wilcoxon
FeedingProportion	Multi-male	Multi-male with female	1.000	1.000	1.00	ns	Wilcoxon
FeedingProportion	Multi-male	Single male with female	1.000	1.000	1.00	ns	Wilcoxon
FeedingProportion	Multi-male with female	Single male with female	0.418	1.000	0.42	ns	Wilcoxon

Supplementary table 1 Wilcoxon signed rank tests between association types (See Fig.1 – Results)

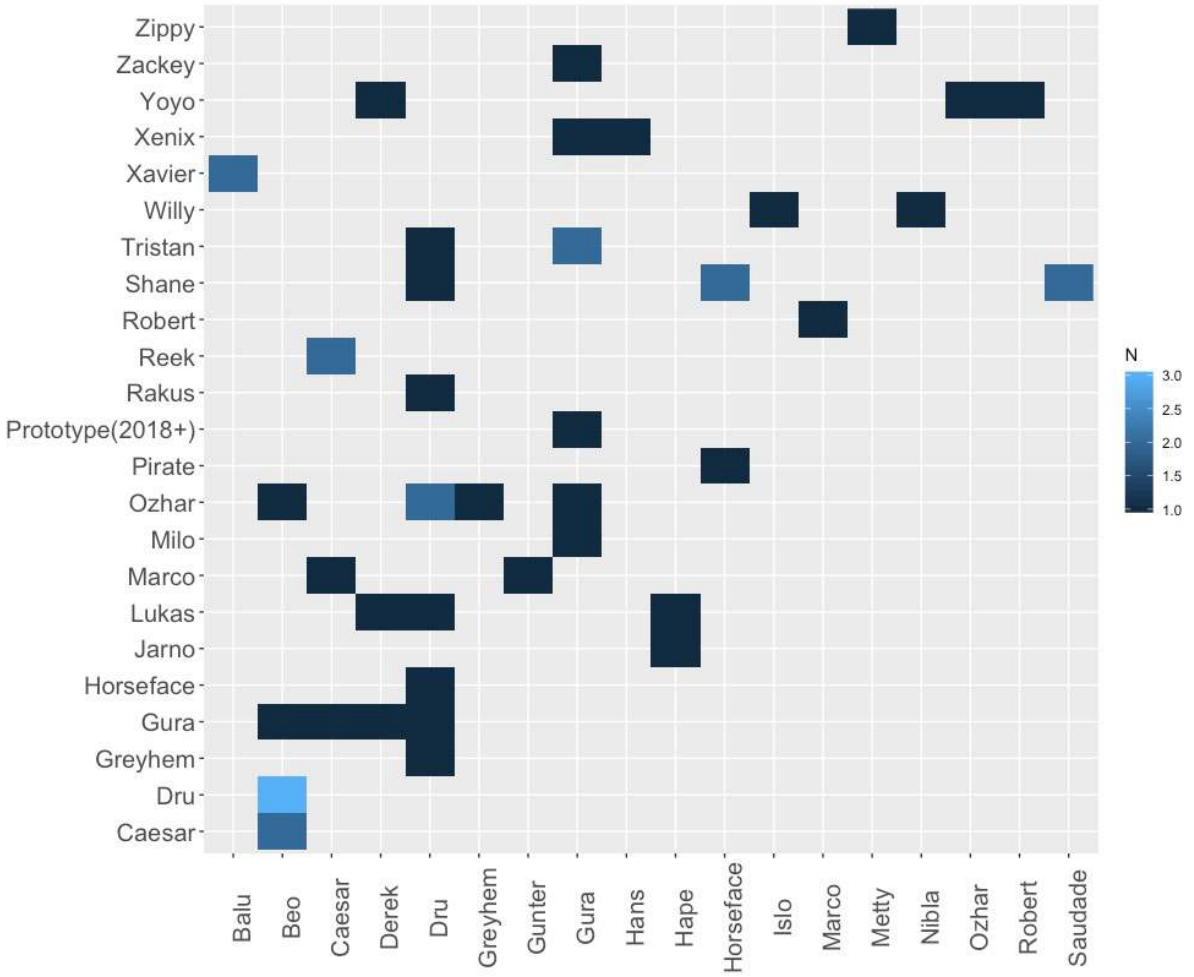
Close proximity rate to unflanged males



Supplementary figure 2 Close proximity rate to unflanged males compared between mutli-male and multi-male female associations.

Focal unflanged males remained in close proximity at the same rate if they were in a multi-male association (only other males were around) or in a multi-male with female association. Unflanged males did seemingly not change the level of tolerance independent of the presence of a female and hence possibility of competition. Also, this helps us to exclude that unflanged males only associate in close proximity around a female. Unflanged males seem to show the same interest of close proximity towards another unflanged male if they are associating without a female.

Individual association rates of unflanged males



Supplementary figure 3 Heat map showing the number of times we observed two identified unflanged males together in an association.

Even though we see that some individuals have associated up to three times we cannot represent data on reoccurring associations between unflanged males. However, if we want to show that unflanged male orangutans form social bonds, we would need to present stable partners over time. In the future we will try to extract data from other focal follows and the information on unflanged males being in association with that focal simultaneously. This way we might be able to show that unflanged males associate frequently with certain individuals.