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Grouping behavior of Sumatran orangutans (*Pongo abelii*) and Tapanuli orangutans (*Pongo tapanuliensis*) living in forest with low fruit abundance

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Abstract

In contrast to the African great apes, orangutans (*Pongo* spp.) are semisolitary: Individuals are often on their own, but form aggregations more often than expected by chance. These temporary aggregations provide social benefits such as mating opportunities. When fruit availability is high, costs of aggregating should be lower, because competition is less pronounced. Therefore, average party size is expected to be higher when fruit availability is high. This hypothesis would also explain why orangutans in highly fruit-productive habitats on Sumatra are more gregarious than in the usually less productive habitats of Borneo. Here, we describe the aggregation behavior of orangutans in less productive Sumatran habitats (Sikundur and Batang Toru), and compare results with those of previously surveyed field sites. Orangutans in Sikundur were more likely to form parties when fruit availability was higher, but the size of daily parties was not significantly affected by fruit availability. With regard to between-site comparisons, average party sizes of females and alone time of parous females in Sikundur and Batang Toru were substantially lower than those for two previously surveyed Sumatran sites, and both fall in the range of values for Bornean sites. Our results indicate that the assessment of orangutans on Sumatra as being more social than those on Borneo needs revision. Instead, between-site differences in sociality seem to reflect differences in average fruit availability.

KEYWORDS

fission–fusion, food competition, great ape, party formation, sociality, socioecology, temporal aggregation

1 | INTRODUCTION

In contrast to the African great ape species, orangutans (*Pongo* spp.) are semisolitary (Mitra Setia, Delgado, Utami Atmoko, Singleton, & van Schaik, 2009). Individuals are often found alone, but form temporary parties more often than expected by chance (Knott et al., 2008; Mitani, Grether, Rodman, & Priatna, 1991; van Schaik, 1999). These parties mainly seem to provide social benefits, such as opportunities to mate, socialize and play, or find protection from harassment (Delgado & van Schaik, 2000; van Schaik, 1999). Also, temporary party formation provides opportunities for social transmission and social learning (Schuppli et al., 2017; van Schaik &

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Knott, 2001). The observed variation in orangutan party size seems to reflect individual-based fission–fusion dynamics (Aureli et al., 2008; van Schaik, 1999) and individuals are often solitary and form relatively small parties because of the high costs of feeding competition.

For other individual-based fission–fusion species, such as spider monkeys (*Ateles* spp.) and chimpanzees (*Pan troglodytes*), multiple studies have documented a significant positive correlation between food abundance and distribution, and party size (Chapman, Wrangham, & Chapman, 1995; Rodrigues, 2017; Shimooka, 2003; Symington, 1988; Wittiger & Boesch, 2013). Fissioning into smaller groups during periods of low fruit availability may reduce travel costs imposed by scramble competition (Snaith & Chapman, 2007). If so, between-population differences in average group size could reflect differences in fruit availability, and within-site temporal variation in group size could correlate with temporal variation in fruit abundance.

Orangutans seem to experience intense scramble competition, which may partly explain their solitary lifestyle (Knott & Kahlenberg, 2010). Scramble competition between orangutans is very likely the result of the distribution of their preferred food sources: They prefer to feed in trees that are relatively small and dispersed compared with other great apes (Fleming, Breitwisch, & Whitesides, 1987; Knott, 1999), and they more often face periods of fruit scarcity (Knott & Kahlenberg, 2010). Multiple findings suggest that orangutans experience and try to avoid scramble competition. For example, Bornean orangutans (*Pongo pygmaeus*) experience longer day ranges when they congregate in parties (Galdikas, 1988) and Bornean orangutan females actively avoid each other (Knott et al., 2008). In addition, Sumatran orangutan (*Pongo abelii*) aggregation size in fig trees matches food abundance in such a way that scramble competition does not occur during aggregations (Utami, Wich, Sterck, & van Hooff, 1997).

Studies on average party size in orangutans have documented a difference between Borneo and Sumatra, with Sumatran orangutans having a larger average party size (Mitra Setia et al., 2009; van Schaik, 1999). In addition, Sumatran orangutans generally spend less time being solitary than those on Borneo (van Noordwijk et al., 2009). This pattern could result from interisland differences in food production. Previously studied Sumatran sites had a higher average fruit availability than those on Borneo (Marshall et al., 2009; Wich et al., 2011). If this pattern is consistent across Sumatra, orangutans there should experience fewer periods of fruit scarcity than orangutans on Borneo, which would reduce scramble competition and consequently the costs of party formation relative to the sites on Borneo (Mitra Setia et al., 2009).

Regarding temporal variation in average orangutan party size within sites, the role of temporal fluctuations in fruit availability remains unclear. Bornean orangutans in Gunung Palung formed more parties during periods of high fruit availability (Knott, 1998), but in Sabangau only, flanged males had an increased average party size when fruit availability was high (Harrison, Morrogh-Bernard, & Chivers, 2010). Similarly, Sumatran orangutans in Ketambe were more likely to form parties, and these parties were larger when fruit availability was higher (Sugardjito, te Boekhorst, & van Hooff, 1987). However, Sugardjito et al. (1987) did not take the duration of parties into account. More recent studies that did include party duration in their analyses found no significant effect of fruit availability on party size in both Ketambe (Wich, Geurts, Mitra Setia, & Utami Atmoko, 2006) and Suaq Balimbing (van Schaik, 1999). However, fruit availability in Ketambe and Suaq Balimbing may always be high enough to offset the costs of party formation (Wich, Geurts et al., 2006).

In addition to temporal differences in average party size, age-sex classes may also differ in their degree of sociality. However, age-sex class differences in sociality seem to vary between sites. While some studies have found no significant differences in sociality between age-sex classes (e.g., van Schaik, 1999), others have found unflanged males (e.g., Wich, Geurts et al., 2006) or nulliparous females (e.g., Galdikas, 1985a) to be the most social. In general, unflanged males and nulliparous females seem to have the highest average party size, while flanged males, especially low-ranking flanged males, have the lowest average party size (Mitra Setia et al., 2009). For unflanged males, forming parties with adult females is an essential part of their reproductive strategy (Galdikas, 1985b; Utami Atmoko & van Hooff, 2004), while sociality of nulliparous females has been explained as contributing to social bonding (Galdikas, 1985a). For flanged males, by contrast, party formation may be very costly, as a result of their large body size (Delgado & van Schaik, 2000; Utami Atmoko & van Hooff, 2004). Lastly, party formation may be costly for parous females because of the energetic demands of motherhood (e.g., lactation). Party formation may, however, offer their infants opportunities to play, which is important for social development (van Noordwijk et al., 2012).

Previous studies of orangutan party size on Sumatra have been conducted mainly in the relatively well-protected and primary forest areas of Ketambe (Wich, Geurts et al., 2006) and Suaq Balimbing (van Schaik, 1999). These sites are prime habitat for orangutans and are generally characterized by low levels of human disturbance and high levels of fruit availability, compared with many Bornean study sites (Husson et al., 2009; Marshall et al., 2009; Wich et al., 2011). Therefore, it is questionable whether the results from these two populations are generalizable to other orangutan populations on Sumatra. Although average orangutan densities are higher on Sumatra than on Borneo (Husson et al., 2009), there also seems to be more variation in the population density on Sumatra (Sumatran range: 0.43–10.18 ind./km^2; Bornean range: 0.31–5.59 ind./km^2; Husson et al., 2009). So, while some Sumatran sites support relatively high estimated densities, many others are characterized by low estimated densities. In some cases, these estimated densities are lower than those of some Bornean field sites.

This study contributes to an understanding of how forest productivity relates to variation in orangutan aggregation by assessing the aggregation behavior of two orangutan populations living in less productive Sumatran forest. These study sites include Sumatran orangutans in Sikundur and the recently described Tapanuli orangutans

in Batang Toru (Nater et al., 2017). These two sites have fruit availabilities that are similar to or even lower than Bornean forests (Knop, Ward, & Wich, 2004; Wich et al., 2014). Both sites are subject to rare supra-annual peaks in fruit production, known as mast fruitings (Wich & van Schaik, 2000). While for Batang Toru, it appears that fruit availability increases only during mast periods, Sikundur shows yearly fluctuations in fruit availability, with the highest fruit availabilities during mast periods.

Our study had three main objectives. First, we aimed to determine whether within-site temporal variation in average party size correlated positively with temporal changes in fruit availability. We expected orangutans to form parties at a higher rate and spend more time in parties during periods of high fruit availability. Second, for the Sikundur data set, we aimed to determine whether aggregation behavior differed between age-sex classes. We expected unflanged males and nulliparous females to be the most gregarious age-sex classes. Flanged males, in contrast, were expected to be the least social age-sex class. Our third objective was to compare average female party size and parous female alone time in less productive Sumatran forest with values for other field sites on Borneo and Sumatra. We expected that average female party size and parous female alone time would be similar to previously reported values for Borneo because fruit availability in Batang Toru and Sikundur is similar to many previously studied Bornean sites. Given that orangutans may increasingly experience low fruit availability as a result of logging, understanding how this affects aggregation behavior is important for orangutan conservation.

2 | METHODS

2.1 | Study areas

The Sikundur study area (3°57′26.4″N/98°04′21.0″E; ca. 6.5 km^2) is located within the Gunung Leuser National Park (Taman Nasional Gunung Leuser) in Northeast Sumatra (Langkat District, North Sumatra Province), which itself is situated within the 2.7 million ha Leuser Ecosystem. The study site is located next to the Besitang River and consists of mixed dipterocarp lowland (30–100 m elevation) forest and alluvial forest along the river (Knop et al., 2004). The area was selectively logged from the late 1960s until the 1980s, and illegal logging still occurs at the borders of the national park; however, the forest has regenerated well enough to house prelogging orangutan densities (Knop et al., 2004).

The Batang Toru Ecosystem consists of roughly 150,000 ha of primary upland forest located in the North-, Central-, and South-Tapanuli Districts, North Sumatra Province (Wich, Fredriksson, Usher, Kühl, & Nowak, 2019). The Batang Toru study area (1°41′9.1″N/98°59′38.1″E; ca. 13.5 km^2, elevation 850–1,100 m; Wich et al., 2014) is positioned in the western forest block and consists of three forest types: heath forest, lowland forest, and mixed dipterocarp forest. Wich et al. (2014) provide a more extensive general description of the local climate and phenology.

2.2 | Behavioral data collection

At both Batang Toru and Sikundur, Yayasan Ekosistem Lestari–Sumatran Orangutan Conservation Programme (YEL-SOCP) employs approximately six full-time local staff members to conduct long-term monitoring of the local orangutan populations. All new staff members were given an introductory period of training (ca. 3 months). Only once they demonstrated a full knowledge of all data collection protocols were they allowed to collect data for the YEL-SOCP long-term database.

Staff members followed individual orangutans from nest-to-nest (dawn till dusk). If there were no individuals to follow after a focal individual was lost or was followed for 10 days in a row, the staff members searched for a new individual. During focal follows, data collection matched the *Orang-utan Data Collection Standardization*, which is commonly used at most orangutan field sites (Morrogh-Bernard, Husson, & McLardy, 2002). Data were collected as instantaneous records of the behavior of focal individuals at 2-min intervals (Altmann, 1974).

During focal follows, assistants recorded the start and end time of each party. We counted the subject as belonging to a party with another orangutan if they were within 50 m of each other. We recognized four age-sex classes (Morrogh-Bernard et al., 2009): (a) unflanged males (UM) were adult males without cheek pads and adolescent males; (b) flanged males (FM) were adult males with cheek pads; (c) adolescent females, who still had small body size, and nulliparous adult females (young sexually active females that did not have an infant yet) were classified as nulliparous females (NF). In general, the absence of an infant is a good indicator of parity in orangutans, because infant mortality rate is extremely low (van Noordwijk et al., 2018; Wich et al., 2004); (d) parous females (PF) had a dependent infant. We did not count dependent offspring as party members, but a dependent individual became an independent individual when its mother gave birth to another offspring (Morrogh-Bernard et al., 2002).

We calculated the focal individual's party size (PS_i) for every focal follow of >3 hr, according to the following formula (van Schaik, 1999; Wich, Geurts et al., 2006):

$$PS_i = 1 + \left(\sum t_{ij}/T_i\right),$$

where T_i is the active period of the focal individual that day, and Σt_{ij} reflects the time that focal individual *i* spent in association with any other independent individual *j*, summed for all *j*s. This formula incorporates both the number of associating individuals and the duration of these associations. A daily party size of 1 means that the focal individual was solitary.

Active periods started with the first activity outside the morning nest and ended with the first resting bout in the evening nest. For days when the focal individual was not followed from nest-to-nest, we defined the active period start and end times as the moments when we first or last saw the focal individual, respectively. We included follows of >3 hr only (Morrogh-Bernard et al., 2002), because

using shorter focal follows may increase Type I error (Harrison, Vogel, Morrogh-Bernard, & van Noordwijk, 2009). We chose the 3-hr cut-off to minimize data loss, especially for Batang Toru, where a more stringent criterion (e.g., 6 hr) would result in almost 20% data loss.

Our final data set for Sikundur comprised 905 focal follows of over >3 hr (June 2013 through May 2015 inclusive; >9,000 observation hours). In total, we observed 17 independent individuals in Sikundur: three unflanged males, seven flanged males, two nulliparous females, and five parous females (Table S1). One of the parous females, Madeline, was a nulliparous female at the start of the study period but gave birth to an infant during the study. Moreover, we observed three independent individuals aggregating with other orangutans, but they were not focal individuals (Table S1).

For Batang Toru, we collected 195 focal follows of over >3 hr for Batang Toru (January 2015 through October 2017 inclusive; >1,800 observation hours). In Batang Toru, six independent individuals were observed: two unflanged males, one flanged male, one nulliparous female, and two parous females (Table S2).

2.3 | Phenological data/fruit availability

We assessed general fruit availability using phenology plots (Marshall & Wich, 2013). For Sikundur, twenty 25 × 25 m plots (total: 1.25 ha), containing approximately 800 stems total, were sampled every month between June 2013 and May 2018. The 20 plots, scattered throughout the area, covered all microhabitat types and the entire elevation range of Sikundur. For Batang Toru, fifteen 10 × 100 m plots (total: 1.5 ha), containing approximately 1,500 stems, were sampled on a monthly basis between March 2009 and October 2017. These plots were evenly spread among the three microhabitat types. For Batang Toru, we used the phenology data that corresponded to the study period (January 2015 through October 2017 inclusive) in our analyses but used the full phenology data set to compute average fruit availability and monthly variation in fruit availability.

At both field sites, trained staff members noted for every liana or tree stem with a diameter at breast height (DBH) of ≥10 cm whether it was bearing fruit. All species were sampled, so no distinction was made between fruits that were or were not part of the orangutan diet, because habitat-wide fruit availability generally correlates strongly with the availability of fruits that orangutans eat (Vogel et al., 2008; Wich, Geurts et al., 2006). Based on the phenological data, we calculated a monthly fruit availability index (FAI) as a proxy for fruit availability. The monthly FAI was the percentage of sampled stems bearing fruit, irrespective of ripeness and quantity.

2.4 | Statistics

All data analyses were carried out in R v.3.5.0 (R Core Team, 2018) and RStudio v.1.1.453 (RStudio Team, 2016). To test for the effect of seasonality on fruit availability in Sikundur and Batang Toru, we used Kruskal–Wallis tests to test for FAI variability across the months of the year. For Batang Toru we ran the analysis twice: both for the study period and for the full period for which phenological data were available (2009–2017). We did this to see whether (lack of) seasonality was apparent only in our relatively short study period, or was characteristic of Batang Toru in general. We used mixed-effect models from the packages lme4 (Bates, Mächler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017) for our analyses, and an alpha level of .05 for all tests. In all analyses, we mean-centered the FAI, to make the intercept more meaningful.

To analyze the data for Sikundur, we used a two-stage hurdle model, consisting of a mixed-effects logistic regression to predict the presence or absence of party formation, and a mixed-effects gamma regression with an inverse link function to predict the daily party size, if a party occurred. We modeled both the presence/absence of party formation and the party size as functions of FAI and age-sex class and added random intercepts per focal individual.

To test whether the probability of party formation and the size of the party differed significantly between age-sex classes in Sikundur, we ran post hoc comparisons using estimated marginal means (emmeans; Lenth, 2019). We used Tukey adjustments to control for multiple comparisons.

For Batang Toru, we used only a mixed-effects logistic regression to predict the presence or absence of party formation. We modeled the occurrence of party formation as a function of FAI. In addition, we added random intercepts for each individual. We did not test for differences in party formation between the age-sex classes because of the low number of focal individuals per age-sex class. In addition, we did not model the size of the party, if a party occurred, as a function of FAI, because parties were formed in only 37 of 195 focal follows.

2.5 | Between-site comparison

Data from previous studies on orangutan party size at other field sites were obtained from Mitra Setia et al. (2009). It is common to report the average female party size when comparing aggregation behavior between sites. To obtain the average female party size, we calculated average daily party sizes per female and took the average of those individual values. For Sikundur, this was based on long-term data of six females (three parous, two nulliparous, one nulliparous/parous), and for Batang Toru this was based on data of three females (two parous, one nulliparous).

Furthermore, we estimated alone time for parous females in Batang Toru and Sikundur by calculating for each parous female how much of their total observation time she spent completely solitary. We used long-term data for four parous females in Sikundur, and two parous females in Batang Toru. We compare these values with the data reported for Suaq Balimbing, Ketambe, Tuanan, and Sabangau in van Noordwijk et al. (2009).

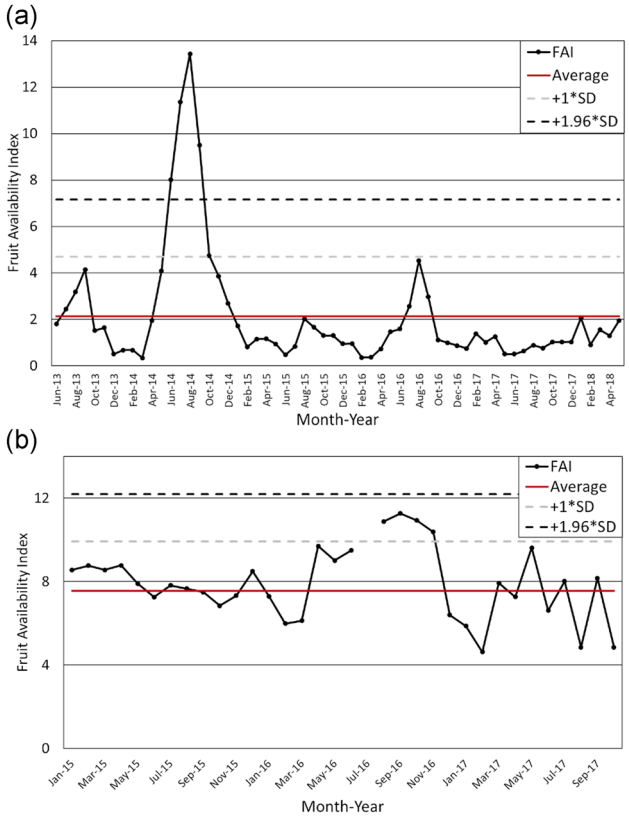

FIGURE 1 Fruit availability index (FAI) in (a) Sikundur between June 2013 and May 2018, and (b) in the Batang Toru area between June 2015 and October 2017. Note that the average FAI and standard deviation (*SD*) were calculated using the data of March 2009 until June 2018. Note that there is one missing value (July 2016)

2.6 | Ethical note

All applicable institutional guidelines were followed, and research complied with the American Society of Primatologists *Principles for the Ethical Treatment of Non-Human Primates*. The research followed all of the regulations of the Ministry of Forestry and Environment for Indonesia and involved only noninvasive observations with well-habituated focal individuals.

3 | RESULTS

3.1 | Sikundur

On average, the FAI in Sikundur between June 2013 and May 2018 was 2.13 (red line; Figure 1). FAI ranged between 0.3 and 13.4 (standard deviation [*SD*] = 2.54). In general, fruit availability was around 1% for most months, with short peaks of 2–5% each year. A Kruskal–Wallis test for seasonality revealed that FAI differed significantly across months of the year ($\chi^2(11) = 25.02$; $p = .009$). Note that one mast fruiting event (FAI of >1.96 × *SD* above average FAI; Wich & van Schaik, 2000) occurred between June 2014 and September 2014.

The logistic model showed a positive relationship between FAI and the probability of party formation (Table 1 and Figure 2). We found no such relationship, however, for the effect of FAI on daily party size in the gamma model (Table 1 and Figure 2).

Age-sex class did not have a significant influence on the probability of party formation ($\chi^2(3) = 5.037$; $p = .169$; Figure 3). Consequently, all post hoc comparisons were nonsignificant (all corrected $p > .17$; Table S3). However, age-sex class did predict the size of formed parties ($\chi^2(3) = 10.488$; $p = .015$; Figure 3). Post hoc tests revealed that unflanged males formed larger parties than flanged males ($z = 2.823$; $p = .025$). All other post hoc tests were nonsignificant after adjusting for multiple comparisons (Table S3).

3.2 | Batang Toru

On average, the FAI in Batang Toru between March 2009 and June 2018 was 7.55 (red line; Figure 1). During the study period (January 2015 to October 2017), there was little variation in FAI between months, and there were no large peaks in fruit availability. Variability in FAI was lower than in Sikundur (*SD* = 1.73). Using the Kruskal–Wallis test, we found no evidence for an effect of month of the year on FAI, in both the full period ($\chi^2(11) = 12.33$; $p = .340$) and the study period ($\chi^2(11) = 11.01$; $p = .443$).

The logistic model did not show a significant relationship between FAI and the probability of party formation in Batang Toru (Table 2 and Figure 4).

3.3 | Between-site comparison

The average female party size was 1.26 for Sikundur and 1.09 for Batang Toru. Both values are substantially lower than previous reports from Sumatra and fall within the range of previous values for Borneo (Figure 5). Furthermore, parous female alone time was similar to Bornean sites as well (Figure 5). Parous females in Sikundur were alone 80% of the time, compared with 91% of the time for parous females in Batang Toru. These results indicate that the grouping behavior of females in less productive Sumatran forest is similar to grouping behavior of females on Borneo, as is the fruit availability.

4 | DISCUSSION

Previous research (van Schaik, 1999; Wich, Geurts et al., 2006) suggested that orangutans on Sumatra are more social than their Bornean counterparts (Mitra Setia et al., 2009), likely as a result of interisland differences in fruit availability (Morrogh-Bernard et al., 2009). However, studies of orangutans on Sumatra occurred in highly productive habitat, which is not representative of the range of habitats that these primates occupy. Studying aggregation behavior in less productive habitats is important to unravel the driving factors behind sociality, as fruit availability may have a profound

TABLE 1 Model output for both the binomial and the gamma mixed model that was applied to the Sikundur data set

	Probability of party formation				Size of formed parties			
	Odds ratio	95% CI	*z* value	*p*	Estimates	95% CI	*t* value	*p*
Predictors								
Intercept	0.37	0.17–0.80	−2.54	**.011**	4.11	2.95–5.74	8.31	**<.001**
FAI (mean-centered)	1.17	1.10–1.25	4.89	**<.001**	0.97	0.94–1.01	−1.61	.107
Age-sex class (NF)	1.51	0.70–3.24	1.05	.294	1.45	0.83–2.51	1.32	.188
Age-sex class (FM)	2.47	0.79–7.76	1.55	.121	1.82	1.07–3.09	2.20	**.027**
Age-sex class (UM)	3.64	1.05–12.60	2.04	**.042**	0.81	0.51–1.27	−0.92	.358
Random effects								
σ^2	3.29				0.54			
τ_{00}	0.72_{Focal}				0.02_{Focal}			
ICC	0.18				0.04			
N	17_{Focal}				16_{Focal}			
Observations	905				342			
Marginal R^2/conditional R^2	.090/.253				.140/.174			

Abbreviations: CI, confidence interval; FAI, fruit availability index; FM, flanged male; ICC, intraclass correlation coefficient; NF, nulliparous female; UM, unflanged male.
Statistically significant values are in bold.

influence on aggregation behavior: Scramble competition in highly productive forests should be less intense, thereby reducing the costs of aggregation.

Our study on orangutans in two less productive Sumatran forests documented average party sizes that were very similar to values for Borneo and substantially lower than those of the Sumatran orangutans in the more productive long-term study sites Ketambe and Suaq Balimbing (Figure 5), thereby challenging the notion that Bornean orangutans are less social than their Sumatran counterparts.

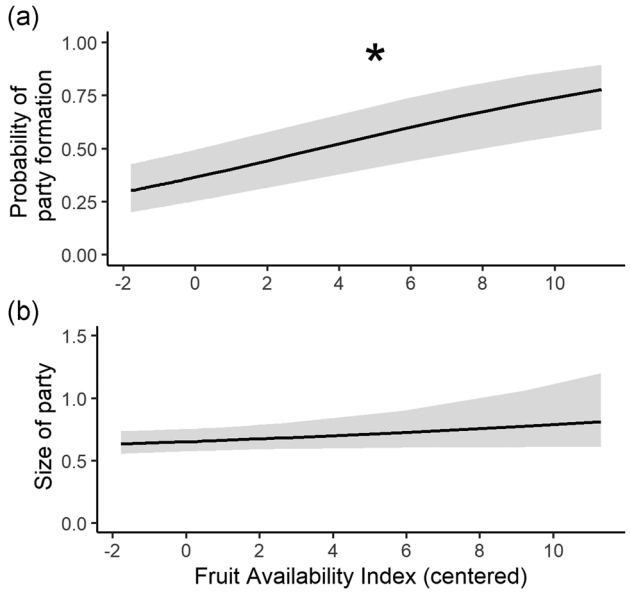

FIGURE 2 Relationship between fruit availability index (FAI; mean-centered) and (a) probability of party formation and (b) daily party size in Sikundur. Shaded area shows 95% confidence interval. *Statistically significant results

Below we discuss the effect of fruit availability (Batang Toru and Sikundur) and age-sex class (Sikundur) on orangutan aggregation behavior, suggest improvements for future studies of orangutan aggregation behavior, and outline conservation implications of our results.

4.1 | Within-site variation in party size

Our hypothesis that aggregation behavior is a plastic response to fruit availability is partly corroborated by the fact that the probability of party formation correlated positively with fruit availability in Sikundur. This result could be interpreted as evidence that higher fruit availability indeed reduces the costs of party formation, thereby increasing the probability of party formation during these periods. However, when parties were formed, the daily party size did not correlate positively with fruit availability. Therefore, it is questionable whether fruit availability also impacts the duration and size of parties. Our results are in line with Sugardjito et al. (1987), who found that increased fruit availability was associated with a higher probability of party formation and larger parties in Ketambe. As mentioned before, Sugardjito et al. (1987) did not take the duration of parties into account, which is an important limitation. Our results are in contrast with other reports from Ketambe and Suaq Balimbing (van Schaik, 1999; Wich, Geurts et al., 2006), where no effect of fruit availability on aggregation behavior was found. These studies may have failed to find such an effect because fruit availability was always high enough to offset the energetic costs of aggregation (Wich, Geurts et al., 2006). However, in less productive habitats like Sikundur, variation in fruit availability may indeed have a considerable impact on aggregation behavior.

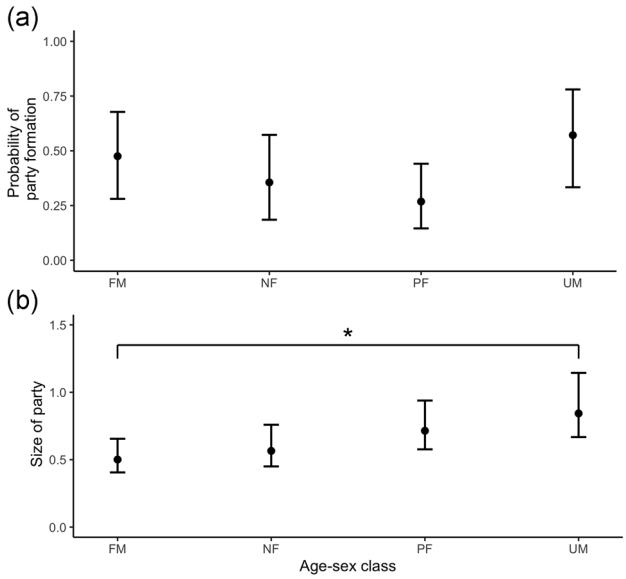

FIGURE 3 Relationship between age-sex class and (a) probability of party formation and (b) daily party size in Sikundur. Error bars show 95% confidence interval. *Statistically significant results. FM, flanged male; NF, nulliparous female; PF, parous female; UM, unflanged male

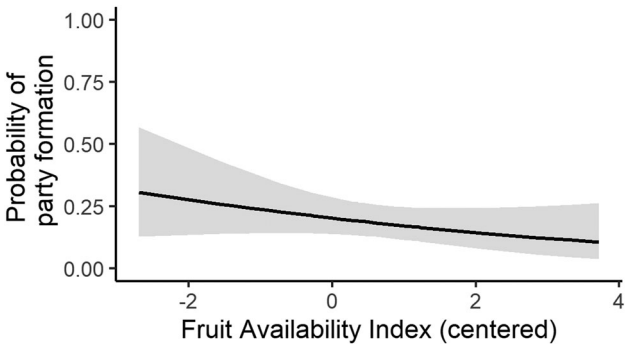

FIGURE 4 Relationship between fruit availability index (FAI; mean-centered) and the probability of party formation in Batang Toru. The shaded area shows the 95% confidence interval

The ambiguity of results on within-site variation in sociality might also have a methodological explanation. First, it could be related to the way we measured fruit availability. An index based on only presence/absence of fruit may be a very rough proxy. In addition to tree DBH and crown size (Chapman et al., 1992), factors such as nutritional quality of available fruit (Busia, Schaffner, Rothman, & Aureli, 2016) and distribution of the available fruit within the habitat (Chapman et al., 1995; Ramos-Fernández, Boyer, & Gómez, 2006) are expected to have a significant influence as well. These measures combined with general presence/absence of food might enhance our understanding of the observed variation in aggregation behavior. Second, social factors may explain a large amount of variation in party size. For example, the identity of the associating individual may influence party formation and duration (e.g., kin or nonkin), the type of party (e.g., consortship, feeding party), and female fecundity may affect party formation. Finally, we note that our Sikundur data set

TABLE 2 Model output for the binomial mixed model that was applied to the Batang Toru data set

	Probability of party formation			
	Odds ratio	95% CI	*z* value	*p*
Predictors				
Intercept	0.26	0.16–0.40	−5.88	**<.001**
FAI (mean-centered)	0.82	0.60–1.12	−1.27	.203
Random effects				
σ^2	3.29			
$\tau_{00\ Focal}$	0.01			
ICC	0.00			
N_{Focal}	6			
Observations	195			
Marginal R^2/conditional R^2	.019/.023			

Abbreviations: CI, confidence interval; FAI, fruit availability index; ICC, intraclass correlation coefficient.
Statistically significant values are in bold.

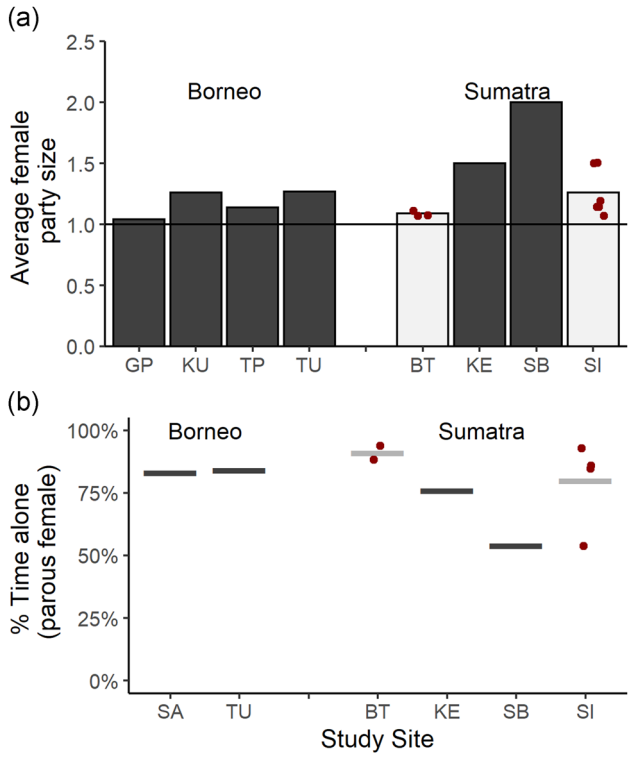

FIGURE 5 Female party size (a) and parous female alone time (b) across Borneo and Sumatra (figures adapted from Mitra Setia et al., 2009 and van Noordwijk et al., 2009, respectively). Previous studies are shown in dark gray, this study in light gray. Dots show values for each individual for SI and BT. BT, Batang Toru; GP, Gunung Palung; KE, Ketambe; KU, Kutai; SA, Sabangau; SB, Suaq Balimbing; SI, Sikundur; TP, Tanjung Puting; TU, Tuanan

contained relatively few data points from periods with high fruit availability. More data from periods of high fruit availability, especially periods of mast fruiting, are necessary to confirm and expand our findings for Sikundur.

In contrast to the Sikundur orangutan population, FAI did not significantly predict party formation in Batang Toru. While this conflicting finding may result from a small sample size, we think this explanation is unlikely, as analysis of the first 2.5 years of Sikundur data still identified a significant correlation between fruit availability and party formation ($z = 4.872$; $p < .001$). An alternative explanation is that FAI variability at Batang Toru was quite low during the study period, making it difficult to detect a pattern in the data. Indeed, the lack of variability would be a plausible explanation, as most data points for Batang Toru had an FAI of between 7 and 9, while FAI values in Sikundur were more evenly distributed in the first 2 years. Previously, large aggregations of Tapanuli orangutans have been observed during the fruiting of *Dacrydium beccarii* trees (Wich et al., 2014). This anecdote indicates that such events may indeed reduce the costs of party formation. Possibly, the fruit availability during our study period was never high enough to reduce these costs, or an increase in party formation may be related to the availability of specific foods of high nutritional quality. Further research would allow for a more thorough investigation into the aggregation behavior of the orangutans in Batang Toru.

4.2 | Age-sex class differences

Contrary to our expectation that unflanged males and nulliparous females would be more social than other age-sex classes in Sikundur, we found little effect of age-sex class on aggregation behavior. Age-sex class did not significantly predict the occurrence of party formation. Unflanged males were most likely to form parties, but the difference with other age-sex classes was not significant. However, we did find that unflanged males had significantly larger daily party sizes than flanged males when they formed parties.

Our results regarding age-sex class differences match the ambiguous results of previous studies. As we have shown, unflanged males tend to be the most social age-sex class, while other age-sex classes are less social and roughly similar to each other. Wich, Geurts et al. (2006) found a similar pattern for Ketambe. However, in Ketambe the average party size of unflanged males was significantly higher than for all other age-sex classes, while we found a significant difference between only flanged males and unflanged males. In that sense, our results are also comparable to previous results from Suaq Balimbing, where average party size did not differ substantially between age-sex classes (van Schaik, 1999).

Contrary to our expectations, nulliparous females were not significantly more social than parous females and flanged males, which contrasts with previous results from Borneo (Galdikas, 1985a). This discrepancy highlights the need for long-term studies. Our current study population contained only two regularly observed nulliparous adult females, of which one gave birth in the second year of observation. Altogether, we had no data on adolescent females that had just become independent of their mothers in our data set. Long-term studies, which are capable of incorporating more individuals over longer periods of time, are essential in evaluating such conflicting results (Kappeler, van Schaik, & Watts, 2012).

4.3 | Between-site comparison

Both in Batang Toru and Sikundur, average female party size was substantially lower than for previously studied orangutan populations on Sumatra but very similar to values for Bornean populations (Figure 5). Furthermore, parous female alone time was similar to previously sampled Bornean sites (Figure 5). These results challenge the notion that orangutans on Sumatra are strictly more social than orangutans on Borneo (e.g., Mitra Setia et al., 2009), and indicate that the perceived interisland differences in orangutan grouping behavior may need revision. Our results add to a growing body of evidence that shows that many of the previously noted differences between orangutans on Borneo and Sumatra are no longer valid (e.g., life history; van Noordwijk et al., 2018).

The main conclusion about the difference in average party size between the islands is that Sumatran populations seem to show much more heterogeneity than those on Borneo. This social variability is consistent with Sumatra being more heterogeneous with regard to fruit availability as well: Some Sumatran sites have relatively high fruit availability (e.g., Ketambe and Suaq Balimbing) (Marshall et al., 2009; Wich et al., 2011) while others have fruit availability indices more similar to (e.g., Batang Toru) or even lower than (e.g., Sikundur) Bornean field sites.

Still, some differences in sociality between sites remain unexplained. For example, Batang Toru has a higher average FAI than Sikundur but has a lower average female party size than Sikundur. This pattern suggests that our FAI does not entirely represent the distribution and availability of food from an orangutan perspective. Second, the fact that FAI is measured differently at different field sites further complicates direct comparisons. While some sites use a simple, general FAI, others use more sophisticated methods, such as sampling orangutan-specific food species, incorporating patch size and maturation stage of the fruits, or incorporating food quality. Such methodological differences may affect the reliability of the between-site comparisons. More consistency in measurement between field sites could facilitate better between-site comparisons. However, we note that multiple studies have documented a high agreement between orangutan-specific FAIs and the more general FAI utilized here (e.g., Vogel et al., 2008; Wich, Geurts et al., 2006).

4.4 | Conservation implications

Studying the behavior of orangutan populations living in less productive habitats such as Sikundur and Batang Toru is important to

understand how orangutans cope with human habitat alteration and how resilient they are to long periods of low fruit availability (Spehar et al., 2018). Many orangutans live outside protected areas (Bornean orangutan: 60–69%; Sumatran orangutan: 0–9%; Tapanuli orangutan: 90–99%) and their habitats will likely become smaller and more fragmented in the future (Ancrenaz et al., 2016; Nowak, Rianti, Wich, Meijaard, & Fredriksson, 2017; Singleton, Wich, Nowak, Usher, & Utami Atmoko, 2017). Logging has a negative impact on fruit availability (e.g., Rao & van Schaik, 1997; Hardus, Lameira, Menken, & Wich, 2012; but see Knop et al., 2004). Similarly, fruit availability decreases with altitude (Djojosudharmo & van Schaik, 1992), which may contribute to the relatively low fruit availability in the Batang Toru area.

While logging does not result in low orangutan densities per se (Borneo: Marshall et al., 2006; Seaman et al., 2019; Sumatra: Knop et al., 2004), behavioral changes that accompany logging suggest increased energetic costs (Hardus et al., 2012; Rao & van Schaik, 1997) or decreased nutrient intake (e.g., increased reliance on fallback foods: Russon, Kuncoro, & Ferisa, 2015) in logged or damaged forest. These behavioral changes may ultimately also influence costly activities, such as party formation. Accordingly, we suggest that future investigations of how logging affects orangutan behavior should also try to incorporate grouping behavior, along with data on diet composition and activity budget. Such data would allow for investigating the direct effect of logging on sociality.

This study shows that orangutans in less productive Sumatran habitat are less social than in highly productive habitat, indicating that lower sociality is a behaviorally plastic response to low fruit availability. How these behavioral changes affect social aspects of the population, such as reproductive behavior and infant development, remains to be established. However, such knowledge is essential for long-term conservation of all three orangutan species.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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