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Abstract: Temporary associations with conspecifics provide critical opportunities for the acquisition and development of socioecological skills, especially in species where these interaction opportunities are not readily available. In fact, social interactions can have far-reaching consequences for the cultural and communicative repertoire on both the species and population level. However, to what extent interaction rates are linked to association patterns, which depend on individual and ecological factors, is often overlooked. Here, we examined the sources of variation in immatures' social behaviour, in relation to both activity and partner type, in one Sumatran (Suaq) and one Bornean population (Tuanan) of wild orang-utans (*Pongo* spp.) that are known to differ in sociability. Specifically, we examined to what extent the time spent in social interactions and with specific social partners was related to study population, but also individual (e.g. age), ecological (food availability) and social variables (e.g. presence of specific associates). Overall, we found that study population and the presence of specific associates (siblings, peers, adult males) had a profound effect on the occurrence of different social activities, while local variation in food availability did not appear to play a major role. Although proportions of time spent in interactions was overall higher at Suaq, we found no difference between the two sites regarding the use of interaction opportunities when partners were available. Begging was mainly directed at mothers, whereas peers and older siblings served primarily as play partners, and unflanged males were frequent targets of social gazing. Our study suggests that orang-utan infants use interaction opportunities differently depending on social partners and interaction type.

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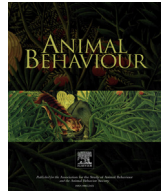


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Social interactions and interaction partners in infant orang-utans of two wild populations

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Temporary associations with conspecifics provide critical opportunities for the acquisition and development of socioecological skills, especially in species where these interaction opportunities are not readily available. In fact, social interactions can have far-reaching consequences for the cultural and communicative repertoire on both the species and population level. However, to what extent interaction rates are linked to association patterns, which depend on individual and ecological factors, is often overlooked. Here, we examined the sources of variation in immatures' social behaviour, in relation to both activity and partner type, in one Sumatran (Suaq) and one Bornean population (Tuanan) of wild orang-utans (*Pongo* spp.) that are known to differ in sociability. Specifically, we examined to what extent the time spent in social interactions and with specific social partners was related to study population, but also individual (e.g. age), ecological (food availability) and social variables (e.g. presence of specific associates). Overall, we found that study population and the presence of specific associates (siblings, peers, adult males) had a profound effect on the occurrence of different social activities, while local variation in food availability did not appear to play a major role. Although proportions of time spent in interactions was overall higher at Suaq, we found no difference between the two sites regarding the use of interaction opportunities when partners were available. Begging was mainly directed at mothers, whereas peers and older siblings served primarily as play partners, and unflanged males were frequent targets of social gazing. Our study suggests that orang-utan infants use interaction opportunities differently depending on social partners and interaction type.

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The sociality and social behaviour (i.e. interactions with individuals in association) of great apes, our closest living relatives, in their natural environments has attracted much research attention over the past few decades. The African apes, and chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*, in particular, are renowned for their relatively large social groups (communities) and complex social relationships (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Hohmann & Fruth, 2002; e.g. ; Nishida, 1968; Watts, 1996). However, the only Asian great ape

genus deviates profoundly from this pattern: orang-utans (*Pongo* spp.) split from the extant African hominoids about 9–13 million years ago (Hobolth, Dutheil, Hawks, Schierup, & Mailund, 2011). The orang-utans' socioecology differs from that of the African apes with respect to an individual-based fission–fusion structure (van Schaik, 1999), female philopatry and male dispersal (Arora et al., 2012; Ashbury et al., 2020; Nater et al., 2011; van Noordwijk et al., 2012). Owing to their rather solitary nature and long inter-birth intervals (van Noordwijk et al., 2018; Wich et al., 2004), it has been presumed that mothers have a particularly large influence on their infants' behavioural development (Bard, 1992). Over the course of infant development, the mother provides the primary model of social and ecological competence, leading to vertical transfer of information critical to survival (Jaeggi et al., 2010;

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Schuppli, Meulman, et al., 2016; van Noordwijk et al., 2009; van Noordwijk & van Schaik, 2005).

Food abundance is thought to limit both population density and gregariousness in orang-utans (van Schaik, 1999; Vogel et al., 2015): temporary associations are energetically costly and lead to fast depletion of food patches (van Schaik, 1999; Wich, Geurts, Mitra Setia, & Utami Atmoko, 2006); their duration is thus limited by energy supply in the habitat (van Schaik, Marshall, & Wich, 2009). The overall higher fruit availability allows for higher association frequency in the well-studied (Northwest) Sumatran populations (i.e. Suaq and Ketambe) compared to Bornean orang-utan study sites (van Schaik, 1999; Wich et al., 2011), whereas sociability may vary throughout the year within populations (van Schaik & Fox, 1996; Wich et al., 2006). Overall, mean party size for adult females (i.e. number of associates including the focal female, but excluding dependent offspring) in the West Sumatran sites were reported to range from 1.5 to 2.0, whereas on Borneo they tended to be around 1.05 to 1.3 (Mitra Setia, Delgado, Utami Atmoko, Singleton, & van Schaik, 2009; van Schaik, 1999). Interestingly, independent immatures and adolescents are the most gregarious age class (Galdikas, 1985; Mitra Setia et al., 2009), which supposedly has far-reaching consequences for postweaning learning opportunities (van Noordwijk et al., 2009). It is now well established that the study populations of Borneo (*Pongo pygmaeus wurmbii*) and Northwest Sumatra (i.e. Suaq and Ketambe, *Pongo abelii*) differ considerably in sociability (cf. Roth, Rianti, Fredriksson, Wich, & Nowak, 2020; van Schaik, 1999) and the number of socially learnt behavioural variants ('sizes of cultural repertoire' (van Schaik et al., 2003; Wich et al., 2012)).

For Bornean orang-utans in particular, studies showed that female associations beyond their dependent and semidependent offspring are constrained by high levels of scramble competition (Knott et al., 2008; Utami Atmoko, Wich, Sterck, & Van Hooff, 1997; van Noordwijk et al., 2012). Energetic costs of association were shown to be higher for female–male than female–female associations (Kunz et al., 2020), which might be a consequence of profound sex differences in ranging patterns and activity budgets (Morrogh-Bernard et al., 2009; Vogel et al., 2017). In contrast to associations with other females (e.g. opportunities for social play for dependent offspring; van Noordwijk et al., 2012), social benefits from associations with males that reach beyond mating opportunities and protection against other males are currently unknown (but see Mörchen, 2016).

Nevertheless, accumulating research efforts over the last few decades have demonstrated that social interactions do play a role in both Bornean and Sumatran orang-utans, particularly for immature individuals (Bard, 1992; Schuppli, Meulman, et al., 2016; van Noordwijk et al., 2012; van Noordwijk & van Schaik, 2005). Remarkably, orang-utans show the highest social learning capacities and the second-largest brain volume (Street, Navarrete, Reader, & Laland, 2017), as well as the highest infant survival (van Noordwijk et al., 2018), of all ape genera. While many of the early interactions, for example in the contexts of play, affiliation, begging or travel coordination, occur within the mother–infant bond (Fröhlich, Lee, Mitra Setia, Schuppli, & van Schaik, 2019; Jaeggi, van Noordwijk, & van Schaik, 2008; Schuppli, Meulman, et al., 2016; van Noordwijk & van Schaik, 2005), interactions with other conspecifics (e.g. older siblings, peers) are observed regularly (Mörchen, 2016; van Noordwijk et al., 2012), albeit at a much lower rate than in the African apes (e.g. Boesch, 1996; Hohmann & Fruth, 2002; Mitani, Watts, & Lwanga, 2002). It has been reported that orang-utans in natural environments make use of associations to play with or learn from conspecifics other than the mother (Schuppli, Meulman, et al., 2016; Schuppli & van Schaik, 2019; van Noordwijk et al., 2009; van Noordwijk et al., 2012; van Schaik, 1999).

An important, but hitherto unaddressed question is to what extent orang-utans 'make use' of interaction opportunities (that is, temporary associations with conspecifics) when they encounter them, or whether associations are characterized by the sheer tolerance of the other individual close by and, for the most part, a lack of interest. Moreover, interaction patterns might look substantially different in relation to activity and partner type in the Bornean and Sumatran populations diverging in sociability (Mitra Setia et al., 2009; van Schaik, 1999). Individuals of the population with fewer temporary associations might have compensating strategies, such as interacting more selectively or at higher rates when specific partners are encountered (at the expense of interactions with mothers and juvenile siblings who are regularly available). However, while orang-utan social interactions have been studied in specific contexts or with certain partners, no study has looked at the interplay of individual, social and ecological factors enabling social interactions in general. Among other aspects of sociality, such data would be critical to make inferences about the link between social and communicative complexity in individuals, populations and species (Fröhlich & van Schaik, 2018). It is still unclear which aspects of 'social complexity' (e.g. group size, number of differentiated relationships or social entropy) could plausibly drive communicative complexity. The close-range communication system of orang-utans is arguably the least studied of the three great ape genera, especially in natural environments (but see Bard, 1992; Fröhlich et al., 2019; Knox et al., 2019). Therefore, establishing to what degree temporary associations are exploited for different social activities with different partners provides a critical basis for future work on orang-utan close-range communication (e.g. Fröhlich et al., 2020).

In the present study, we aimed to address this gap by investigating infants' social interactions in two orang-utan populations (*P. abelii* at Suaq, Sumatra, and *P. pygmaeus wurmbii* at Tuanan, Borneo). As discussed above, Suaq has a higher level of sociability and social tolerance (Mitra Setia et al., 2009; van Schaik, 1999) and also a higher population density than Tuanan (Husson et al., 2009). Recently, Schuppli, van Noordwijk, Utami Atmoko, and van Schaik (2020) demonstrated that more sociable orang-utan mothers have more exploratory offspring, suggesting early exposure to more potential role models may have a lasting effect.

Therefore, we asked whether reported differences between the populations are reflected in interaction rates or, in other words, whether Suaq orang-utans make use of these high association rates. On the other hand, immatures in Tuanan might exhibit higher interaction rates during associations and thus exploit opportunities for social interactions more (Kunz, 2015), which is why we controlled for the availability of social partners in our study. Earlier studies have shown that female–female associations (and even encounters for females with similar home range overlap) are biased towards kin (Knott et al., 2008; Singleton & van Schaik, 2002; van Noordwijk et al., 2012). Nevertheless, for immature individuals, associations of any type (including adult males, older siblings and peers) may differ in their suitability as interaction opportunities. For example, we predicted that associations with other mother–offspring pairs are particularly relevant for play interactions (van Noordwijk et al., 2012), whereas adult males potentially offer social learning opportunities (Mörchen, 2016). Since unflanged males (sexually mature but lacking fully developed secondary sexual characteristics) disperse out of their natal area, they might act as 'cultural vectors' for nondispersing females and their offspring.

To address these questions, we investigated to what extent association type, study population and other potentially confounding variables predict infants' interactions regarding both interaction type and partners/targets. Specifically, we focused on individual

(e.g. age, sex and matriline size), social (e.g. study site, number of associates other than the mother and closest-in-age sibling, association with siblings and adult males) and ecological effects (i.e. fruit availability) on time spent (1) in different types of interaction (e.g. social play, social gaze and begging) and (2) with different partners, controlling for their availability.

METHODS

Study Sites

We observed orang-utan populations of wild Sumatran (*P. abelii*) and Bornean orang-utans (*P. pygmaeus wurmbii*) at the long-term research sites of Suaq Balimbing (03°02'N, 97°25'E, Gunung Leuser National Park, South Aceh, Indonesia) and Tuanan (02°15'S, 114°44'E, Mawas Reserve, Central Kalimantan, Indonesia), respectively. Both study sites consist mainly of peat swamp forest with relatively high orang-utan densities, with an estimated seven individuals per km² at Suaq and four at Tuanan (Husson et al., 2009; Singleton, Knott, Morrogh-Bernard, Wich, & van Schaik, 2009). Subjects for this study consisted of four Sumatran and seven Bornean orang-utan infants. Infant ages were either known because the birth was observed or estimated from the first time an infant was observed (definitions cf. van Noordwijk et al., 2018; see Tab. 1 for detailed information on subjects).

Data Collection and Processing

Focal observations of infants were conducted between February 2011 and October 2018 (Suaq Balimbing: February 2011–October 2018; Tuanan: April 2014–July 2018), and consisted of full (nest-to-nest) or partial follows (e.g. nest-to-lost or found-to-nest, no minimum duration) of mother–offspring pairs. We extracted data only from this period, to ensure consistent data quality and because these infants were the subjects of concurrent research on close-range communication (e.g. Fröhlich et al., 2020). Behavioural data were collected following an established protocol for orang-utan data collection (<https://www.aim.uzh.ch/de/orangutannetwork/sfm.html>), using focal animal sampling. All observers were trained to use this protocol and interobserver reliability tests were conducted after each training phase. Some observers (including C.S., J.K., S.F. and M.F.) collected data at both study sites ensuring the use of the same criteria during training. Using instantaneous scan sampling at 2 min intervals, we recorded the activity of the focal individual and the identities of all association partners (i.e. all conspecifics within 50 m), and for social interactions, the interaction partner as well as several other parameters (e.g. height, visibility and weather; for details of data collection protocol see website above). We included only social interactions scored as

activity in these scans (i.e. only social interactions that lasted longer than 5 s), thus excluding scans with poor visibility (scored as '0') and brief interactions completed between two scans (our data therefore do not capture all occurrences of social interactions). This resulted in a total of 128 918 (Suaq: 72 165; Tuanan: 56 753) scan sample points (mean ± SD per infant = 11 719.8 ± 6968.9) collected on 440 (Suaq: 267; Tuanan: 173) follow days (mean ± SD per infant = 40 ± 25.7), corresponding to roughly 4297 h of observation (see Table 1 for an overview of data obtained per subject).

For the inferential analyses, we subsequently coded the data set for the following variables: age difference (peer or same-aged partner: age difference of less than 1 year if the focal individual was younger than 2 years, or less than 3 years if it was older than 2 years; older partner: age difference of more than 1 or 3 years if the focal individual was younger or older than 2 years, respectively) kin relationship with interaction partner (mother, older maternal sibling) and matriline size (number of adult females/mothers in matriline). Although social interactions also included grooming, agonistic interactions, sexual contact, travel initiations and affiliation (i.e. seeking physical contact involving behaviours like embracing, hand holding and touching), their occurrence was too rare (i.e. < 200 cases each, 935 cases in total = 0.7% of all observations) for separate inferential analyses. We therefore focused on social play (i.e. repetitious behaviour out of 'serious' contexts that does not serve an immediate purpose (Bekoff & Byers, 1998), mostly arboreal play wrestling), social gaze (i.e. intently looking at conspecific without major movements or other behaviours involved, including peering and watching as used by Schuppli, Forss, et al. (2016) and Schuppli, Meulman, et al. (2016)) and begging (i.e. food solicitation via requests and attempts to take food). The fruit availability index (FAI) was calculated as the mean percentage of trees with ripe fruits within the habitat in a given month, based on phenology plots containing around 1000 trees (range = 0.27–16.6; Vogel et al., 2008) and z-transformed within study site (since Suaq's fruit availability is known to be generally higher).

Statistical Analyses

We used generalized linear mixed models (Baayen, 2008) with a binomial error structure and logit link function to test the effects of individual and social factors on (1) the overall occurrence of social activities with any partner over all scans (all, social play, social gaze and begging) and (2) the occurrence of social interactions with specific partners given they were in the same party and thus available (mothers, siblings, peers, older immatures, unflanged males). The model for 'all' interactions included play, gaze and begging interactions, but also other social activities that were too rare to be considered separately. For all models, we included site

Table 1
Overview of subjects and data sets

ID	Site	Sex	Age range (months)	Matriline size	No. of follow days	No. of observations (2 min scans)
Cinnamon	Suaq	F	14–78	Large	51	13 818
Eden	Suaq	F	0–44	Large	54	14 338
Frankie	Suaq	M	9–67	Large	67	18 102
Lois	Suaq	M	6–94	Large	95	25 907
Caka	Tuanan	M	22–43	Small	8	2686
Darwin	Tuanan	M	16–23	Small	11	3780
Jane	Tuanan	F	9–60	Large	47	15 302
Ketambe	Tuanan	M	22–46	Large	21	6182
Merkur	Tuanan	M	5–27	Large	18	5163
Moby	Tuanan	F	17–41	Large	21	6830
Tuk2	Tuanan	M	46–74	Small	47	16 810
Total	4:7	4:7	0–94	3:8	440	128 918

F: female; M: male.

(two levels: Suaq and Tuanan), infants' age (in months, range 0–94), sex (two levels: female, male) and matriline size (two levels: small = two or fewer adult females in matriline, large = more than two adult females in matriline) as our key test predictors. Since we assumed that age effects might be nonlinear for infants' interactions based on previous work on these populations (Schuppli, Meulman, et al., 2016; van Noordwijk et al., 2012), we included age as unsquared and squared terms in the model. In the first set of models including all scan samples (1) we also included association type (three levels: older sibling in association, at least one peer in association, at least one adult male in association) as a test predictor, to test whether these specific associates affected the occurrence of interactions (further possible association types were not included to keep the model complexity at an acceptable level). In the second set of models controlling for the availability of specific types of interaction partners (2), we included party size (i.e. number of associates without the mother and her offspring, range 0–7) instead of association types as predictor in the models (this variable was not included in the first set due to high collinearity with the factor level 'peers in association'). To control for a possible effect of FAI, we also included it as a further fixed effect in the models. As random effects (intercepts) we included infant identity, follow date (to account for different conditions for data collection, e.g. weather, forest area, potential associates) and observer identity in the model. To keep type 1 error rates at the nominal level of 5%, we also included the random slopes components of age, FAI, as well as levels of party composition (only the first set of models) and party size (only the second set of models) within subject ID (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009).

For the response variables considered in our models, especially the occurrence of social play, it was likely that they would show temporal autocorrelation (observations lying close to one another in time being on average more similar to one another than more distant observations). If such autocorrelation also exists in the residuals of the model, this would violate the assumption of independent residuals. We thus incorporated the autocorrelation explicitly in our models (see also Gomes, Mundry, & Boesch, 2009; Head, Robbins, Mundry, Makaga, & Boesch, 2012). We did this by running the full model as described above and extracting the residuals from it. We then, separately for each data point, determined the weighted average of all other data points of the same respective individual and included the derived variable as an additional fixed effect in the model. The weight was a function of the temporal difference between the two data points. More specifically, the weighting function had the shape of a Gaussian distribution with a mean of zero (maximum weight at distance equal to zero) and the standard deviation determined such that the likelihood of the full model including the autocorrelation was maximized.

All models were implemented in R (v3.4.1, R Development Core Team, 2017) using the function `glmer` of the package `lme4` (Bates, Maechler, Bolker, & Walker, 2014). To test the overall significance of our key test predictors (Forstmeier & Schielzeth, 2011; Mundry, 2014), we compared the full models with the respective null models comprising only the control predictor as well as all random effects using a likelihood ratio test (Dobson, 2002). Prior to running the models we z-transformed age and party size (Aiken & West, 1991; Schielzeth, 2010). To control for collinearity, we determined the variance inflation factors (VIF; Field, 2005; Quinn & Keough, 2002) from a model including only the fixed main effects using the function `vif` of the R package `car` (Fox & Weisberg, 2011). This revealed collinearity to not be an issue (maximum VIF = 1.9). Confidence intervals were derived using the function `sim` of the R-package `arm` (Gelman & Su, 2014). Tests of the individual fixed

effects were derived using likelihood ratio tests (R function `drop1` with argument 'test' set to 'Chisq').

Ethical Note

Data collection was purely observational and noninvasive, with focal scan samples taken from a minimum distance of 10 m, in an effort to avoid influencing the natural behaviour of the individuals and populations. The research followed the recommendations of the 'Animals (Scientific Procedures) Act 1986', as published by the U.K. government, and the principles of 'Ethical Treatment of Non-Human Primates' as stated by the American Society of Primatologists. Approval for this study was gained from the Indonesian State Ministry for Research and Technology (RISTEK), the Directorate General of Natural Resources and Ecosystem Conservation-Ministry of Environment & Forestry of Indonesia (KSDAE-KLHK), the Ministry of Internal Affairs, the Nature Conservation Agency of Central Kalimantan (BKSDA KalTeng) and the Gunung Leuser National Park (BBTNGL).

RESULTS

Engagement in Different Social Activities

On average, social interactions were recorded in $5.1 \pm 2.1\%$ of focal observation time (individual mean \pm SD; Suaq: $7.2 \pm 0.9\%$; Tuanan: $3.9 \pm 1.7\%$; for details on all social interactions see Table 2 and Fig. 1). Overall, the respective full models including the key test predictors (i.e. study site, age, sex, matriline size and associates) fitted the data better than the null models, revealing a significant impact of these variables (likelihood ratio tests for social interactions: all combined: $\chi^2_8 = 1382.646$, $P < 0.001$; playing: $\chi^2_8 = 1605.812$, $P < 0.001$; gazing: $\chi^2_8 = 81.5$, $P < 0.001$; begging: $\chi^2_8 = 33.115$, $P < 0.001$; $N = 105$ 192). The occurrence of social interactions overall (that is, the proportion of time spent in interactions in general, and specifically in social play, gazing and begging), was more likely at Suaq than Tuanan (Table 3, Fig. 1). We found a negative quadratic age effect on the occurrence of play interactions, meaning that the proportion of time spent playing decreased in older infants. The proportion of time spent begging also decreased with age (i.e. negative linear effect), but this effect was attenuated in older infants (i.e. positive quadratic effect, Table 3). The proportion of time spent in a social interaction overall and playing increased with an older sibling or peer in association (Table 3), whereas the proportion of time spent in social gazing was significantly higher with the presence of a peer or at least one adult male (Table 3). Apart from the autocorrelation term, none of the other effects in the models had a significant impact on the response variables.

Table 2

Mean percentage of time spent in social interaction in relation to social activity and interaction partner (controlled for availability) at both study sites (mean \pm SD)

	Suaq	Tuanan	Total
<i>Social activity</i>			
All	7.2 \pm 0.9	3.9 \pm 1.7	5.1 \pm 2.1
Play	4.2 \pm 1.4	2.4 \pm 1.6	3.0 \pm 1.8
Gaze	1.7 \pm 0.5	0.7 \pm 0.2	1.1 \pm 0.6
Beg	0.5 \pm 0.1	0.5 \pm 0.3	0.5 \pm 0.3
<i>Interaction partner</i>			
Mother	2.7 \pm 0.4	2.1 \pm 1.0	2.3 \pm 0.9
Sibling	4.3 \pm 3.9	2.0 \pm 1.8	3.0 \pm 3.1
Peer	16.9 \pm 13.2	18.7 \pm 19.2	17.9 \pm 17.1
Older immature	15.8 \pm 8.8	4.7 \pm 8.8	9.1 \pm 10.3
Unflanged male	3.2 \pm 1.6	1.9 \pm 1.7	2.4 \pm 1.8

Interactions with Different Partners

On average, social interactions with mothers were recorded in $2.3 \pm 0.9\%$ of focal observation time. Within the total observation time, associations with a sibling occurred in 13.9%, with peers (other mother–offspring pairs) in 5.1%, with older (nonsibling) immatures in 3.9% and with unflanged males in 16.6% of time. When we controlled for the availability of specific partners, infants interacted with siblings for $3.0 \pm 3.1\%$ of this time, with peers for $17.9 \pm 17.1\%$, with older immatures for $9.1 \pm 10.3\%$ and with unflanged males for $2.4 \pm 1.8\%$ (see Table 2 and Fig. 2 for site-specific results). Begging and gazing were mostly directed at mothers, whereas interactions with siblings, peers and older immatures were mostly in the form of active social play (Fig. 3). In interactions with unflanged males these were mostly (passive) targets of social gazing (Fig. 3). The likelihood ratio tests revealed that the key test predictors (i.e. study site, age, sex, cluster size, party size) had a significant impact on the occurrence of interactions with mothers, peers and older immatures (mothers: $\chi^2_6 = 19.197$, $P = 0.004$, $N = 105\ 190$; peers: $\chi^2_6 = 12.881$, $P = 0.045$, $N = 5364$; older immatures: $\chi^2_6 = 15.303$, $P = 0.018$, $N = 4079$), but not those with siblings and unflanged males (siblings: $\chi^2_6 = 9.612$, $P = 0.142$, $N = 14\ 570$; unflanged males: $\chi^2_6 = 4.491$, $P = 0.611$; $N = 17\ 441$). When controlling for availability of interaction partners, we found that the proportion of time spent in interactions with mothers was lower in Tuanan and decreased with the number of associates other than mother and sibling (Table 4). The proportion of time spent in interactions with older immatures also decreased with the number of associates (Table 4). Apart from the autocorrelation term, none of the other effects in these two models had a significant impact on the response variables.

DISCUSSION

The specific social activities and targets of early interactions have rarely been studied in species where interaction opportunities are constrained by ecological factors. Compared to other primate species, opportunities for orang-utan infants to interact with peers and older conspecifics are relatively rare (van Noordwijk et al., 2012). In this study, we aimed to test to what extent individual, social and ecological factors predict social interactions in orang-

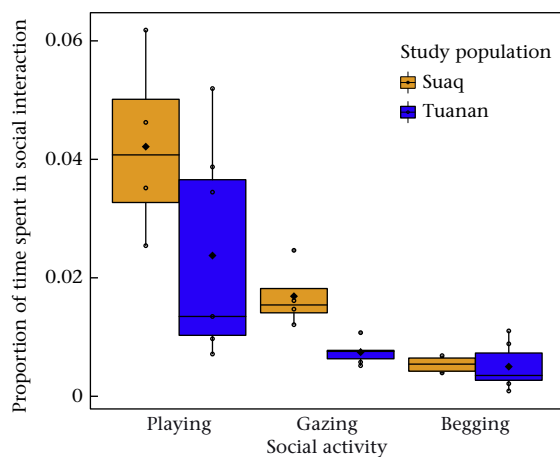


Figure 1. Proportion of time spent on different social activities in relation to study site. Box plots show individual means (open circles), population means (filled diamonds), medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (filled dots).

utan infants of two species and populations that are well known to differ in sociability (Mittra Setia et al., 2009; van Schaik, 1999).

Overall, our results showed that the variation in the time spent in social activity was mainly predicted by site and the type of associates. While controlling for important individual and ecological variables, we found that an infant's time spent in social interactions, and specifically in social play, gazing and begging, was higher at Suaq, the more sociable population. Hence, while it was already known that Suaq orang-utans are more gregarious, we have shown here that they also make use of these higher association rates by spending more time in different social interactions than those of Tuanan. When controlling for the availability of the respective social partners, we did not find significant site differences regarding the use of interaction opportunities; in other words, when potential partners were in association, infants of both populations seemed to interact with them at comparable rates (cf. Kunz, 2015). However, the proportion of time spent playing socially

Table 3

Effects of individual, social and ecological variables on the occurrence of all social interactions, playing, gazing and begging derived using GLMMs with a binomial error structure and logit link function ($N = 105\ 192$)

	Estimate	SE	χ^2_1	<i>P</i>
All interactions				
Intercept	-4.385	0.257	—	—
Site [Tuanan]	-1.005	0.354	6.970	0.008
Age	0.109	0.234	0.220	0.637
Age ²	0.065	0.084	0.600	0.440
Sex [Male]	0.145	0.184	0.610	0.435
Matriline size [large]	-0.153	0.137	1.270	0.261
Associates [sibling]	1.276	0.106	145.39	< 0.001
Associates [male]	-0.122	0.370	0.110	0.743
Associates [peer]	2.604	0.078	1308.39	< 0.001
FAI	-0.060	0.105	0.320	0.574
AC term	0.433	0.014	967.03	< 0.001
Playing				
Intercept	-6.255	0.408	—	—
Site [Tuanan]	-1.274	0.491	4.914	0.027
Age	0.043	0.338	0.004	0.947
Age ²	-0.368	0.150	5.417	0.020
Sex [Male]	0.504	0.402	1.379	0.240
Matriline size [large]	0.096	0.244	0.145	0.703
Associates [sibling]	2.290	0.156	231.237	< 0.001
Associates [male]	-0.470	0.583	0.623	0.430
Associates [peer]	3.546	0.110	255.52	< 0.001
FAI	-0.259	0.202	1.260	0.262
AC term	0.652	0.020	1402.866	< 0.001
Gazing				
Intercept	-5.751	0.327	—	—
Site [Tuanan]	-1.161	0.407	7.048	0.008
Age	0.178	0.154	1.315	0.252
Age ²	0.176	0.093	3.318	0.069
Sex [Male]	-0.016	0.237	0.005	0.943
Matriline size [large]	-0.239	0.137	3.040	0.081
Associates [sibling]	0.219	0.177	1.428	0.232
Associates [male]	0.709	0.177	7.834	0.005
Associates [peer]	1.120	0.140	59.301	< 0.001
FAI	0.016	0.176	0.008	0.928
AC term	0.275	0.019	168.079	< 0.001
Begging				
Intercept	-7.001	0.329	—	—
Site [Tuanan]	-0.812	0.384	3.977	0.046
Age	-0.541	0.178	5.349	0.021
Age ²	0.312	0.107	8.602	0.003
Sex [Male]	0.453	0.235	2.937	0.087
Matriline size [large]	0.175	0.163	1.009	0.315
Associates [sibling]	0.286	0.270	1.117	0.291
Associates [male]	0.220	0.186	1.376	0.241
Associates [peer]	-0.455	0.323	2.113	0.146
FAI	0.043	0.161	0.070	0.792
AC term	0.329	0.036	69.164	< 0.001

FAI: fruit availability index; AC term: autocorrelation term. Significant effects ($P < 0.05$) are depicted in italics.

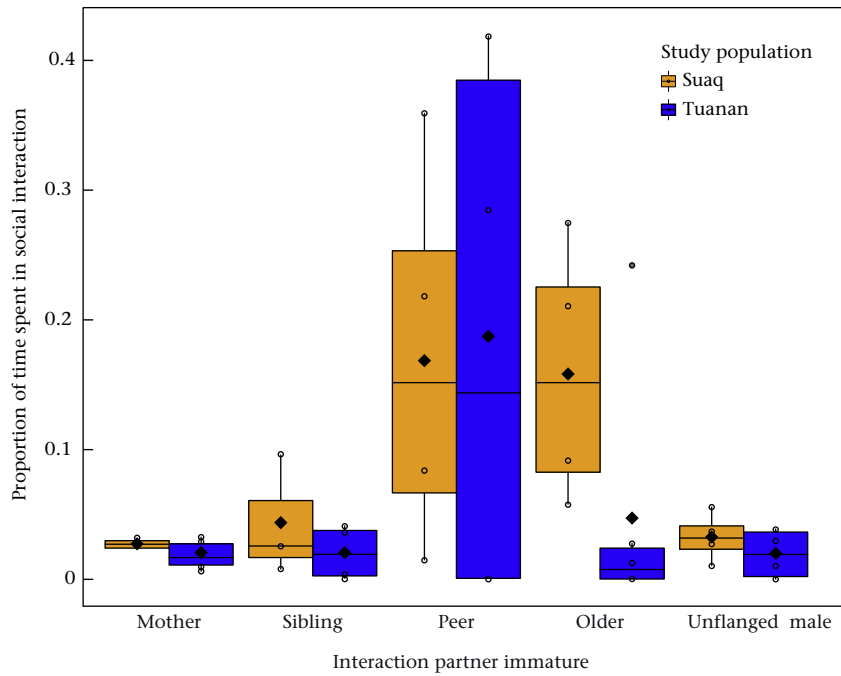


Figure 2. Proportion of time spent in social interaction with different partners (controlled for availability) in relation to study site. Box plots show individual means (open circles), population means (filled diamonds), medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (filled dots).

with peers when available was on average higher in Tuanan, although the variation between individuals was high. Some Tuanan infants thus seemed to compensate to some extent for the rarity of the opportunity to play with peers, and more representative sample sizes are needed before final conclusions can be drawn. The presence of peers and closest-in-age sibling overall increased the occurrence of social interactions, including social play. On the other hand, social gaze was positively associated with the presence of

adult males. Begging interactions occurred almost exclusively with mothers and were more likely in younger than older infants. Importantly, interactions with mothers were less likely as more conspecifics were in association. Social play was the most common social interaction with older siblings and peers. In our data set, relative food availability seemed to play no critical role for the activities and targets of interactions.

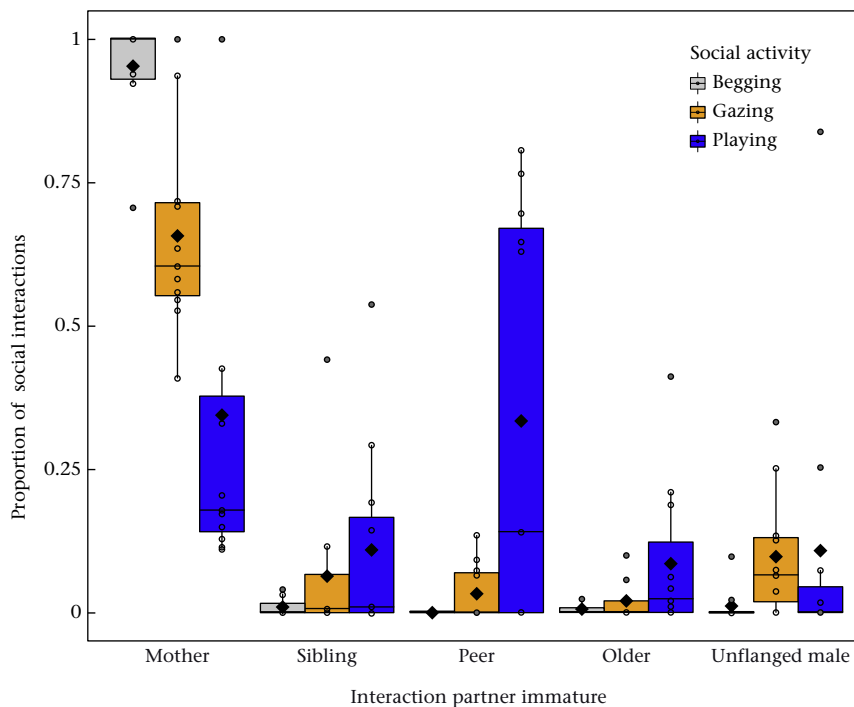


Figure 3. Proportion of social interactions with different partners in relation to social activity. Box plots show individual means (open circles), population means (filled diamonds), medians (horizontal lines), quartiles (boxes), percentiles (2.5% and 97.5%, vertical lines) and outliers (filled dots).

Table 4

Effects of individual, social and ecological variables on the proportion of time spent in interactions with mothers ($N = 105\ 190$) and older immatures ($N = 4079$) derived using GLMMs with a binomial error structure and logit link function

	Estimate	SE	χ^2_1	<i>P</i>
Mothers				
Intercept	-4.551	0.264	—	—
Site [Tuanan]	-1.286	0.326	11.500	0.001
Age	-0.167	0.139	1.290	0.257
Age ²	0.043	0.074	0.320	0.569
Sex [Male]	0.242	0.215	1.390	0.239
Matriline size [large]	0.005	0.125	0.000	0.977
No. of associates	-0.245	0.078	6.640	0.010
FAI	-0.002	0.100	0.000	0.983
AC term	0.371	0.018	378.700	<0.001
Older immatures				
Intercept	-2.54	1.145	—	—
Site [Tuanan]	-1.625	1.754	0.770	0.380
Age	1.256	0.761	1.450	0.228
Age ²	0.246	0.510	0.230	0.633
Sex [Male]	-2.734	1.052	2.090	0.148
Matriline size [large]	0.544	0.623	0.770	0.379
No. of associates	-0.956	0.442	4.360	0.037
FAI	0.883	0.535	3.030	0.082
AC term	0.999	0.057	416.300	<0.001

FAI: fruit availability index; AC term: autocorrelation term. Significant effects ($P < 0.05$) are depicted in italics.

Play was by far the most common social activity among infants, especially with peers, older immatures and closest-in-age siblings. Although immatures spent only a small fraction of their overall time budget in social play, even at Suaq, the most gregarious orang-utan population with the largest average party sizes (Fox, van Schaik, Sitompul, & Wright, 2004; van Schaik, 1999), the strong effect of sibling and peer presence shows that infants seemed to take advantage of specific play opportunities (see also van Noordwijk et al., 2012). This is reflected in the finding that mother–infant interactions were more likely when association sizes were small. The same effect was found for infant–older immature interactions, which might be due to independent immatures preferentially playing with infants when no or few other conspecifics were around. Our results showed that older siblings that still regularly associated with the mother–offspring dyad seemed to represent important play partners for the infant. Although the presence of older siblings had a positive effect on the time spent in social interaction and play in this study (when they were around, infants seized the opportunity for social play), these are not readily available for play sessions. If present, siblings are often at least 7 years older due to the large interbirth intervals in orang-utans, and thus no longer qualify as same-sized play partners (van Noordwijk et al., 2018). They are no longer in frequent association by the time the infant is more spatially independent and able to engage in social play. Peers and older immatures therefore also qualify as important play partners for orang-utan infants. It has been shown that, since adult parous females rarely engage in social exchanges (such as grooming or food sharing) and associations bear the cost of potential scramble competition (Knott et al., 2008; Kunz et al., 2020; Utami Atmoko et al., 1997), associations among familiar females seem to be primarily for the offspring's interest; these play opportunities for infants constitute an important benefit of female philopatry in orang-utans (van Noordwijk et al., 2012). Besides facilitating the development of motor and brain functions (e.g. Bekoff & Byers, 1998; Berghänel, Schülke, & Ostner, 2015; Byers & Walker, 1995; Montgomery, 2014; Pellis & Pellis, 2007), social play might also be vital for preparing the immature for unpredictable outcomes with unfamiliar conspecifics later in life (Fröhlich, Wittig, & Pika, 2016; Spinka, Newberry, & Bekoff, 2001; Weller, Camerlink, Turner, Farish, & Arnott, 2019).

Apart from the mother, unflanged males were targets of social gaze behaviour; in fact, most of the social interactions involving unflanged males involved just gazing. It is well established that social peering and watching play a substantial role as social learning opportunities in orang-utans (Adams, 2005; Schuppli, Meulman, et al., 2016). Building on the studies of Jaeggi et al. (2010; 2008), Schuppli, Forss, et al. (2016) and Schuppli, Meulman, et al. (2016) reported that by 5 years of age (close to weaning), young orang-utans showed a clear preference for non-mother role models when peering at conspecifics. Previous studies at Suaq and Tuanan suggested that young orang-utans not only rely on peering at their mother's activities (Schuppli, Meulman, et al., 2016), but with increasing age might also develop a preference for watching immigrant unflanged adult males' activities, especially in the nesting and social contexts (Mörchen, 2016). Since males leave their natal range (Nietlisbach et al., 2012), it has been speculated that unflanged males may act as 'cultural vectors'. Thus, males would facilitate the transfer of traditions among female social networks, such as specific food-processing techniques (e.g. seed extraction tool use) and communicative signals (e.g. tool-assisted kiss-squeaks; van Schaik et al., 2003; Wich et al., 2012). However, associations with males are rare, probably because male–female associations and social interactions appear to be energetically costly to females, especially at Tuanan as illustrated by males initiating and maintaining such associations much more consistently than females (Kunz et al., 2020). It is also critical to consider that unflanged males are probably more readily available when infants are older, as they associate more frequently with the mothers with increasing likelihood of conception of the next offspring (Kunz, 2020; van Schaik, 1999).

In contrast to social play and gaze, begging was almost exclusively directed at mothers. It has been suggested that this behaviour plays a key role for practice and development of intentional signal use in young orang-utans (Bard, 1992). For begging by immatures, both nutritional and informational functions of mother–offspring food transfers have been discussed (Jaeggi et al., 2008), so it is not surprising that the proportion of begging was lower in older infants. This also fits with the finding that Tuanan infants spent less time interacting with their mothers. Begging can be for food or for information; thus, if there is less to learn due to a more limited diet containing fewer complicated or rare items, infants also need to beg less (see Schuppli, Forss, et al., 2016). Thus, differences in begging rates do not necessarily mean that infants do not take advantage of opportunities for what they need.

In contrast to the African apes, allogrooming and other affiliative interactions seem to occur only rarely among wild orang-utans, even within mother–offspring bonds (MacKinnon, 1974; van Noordwijk et al., 2009). While mothers do groom their young offspring, these interactions were too infrequent to conduct reliable inferential analyses. The social function (derived from the hygienic one) appears to be especially pronounced in species that originally had a high need for it, i.e. terrestrial ones (Grueter, Bissonnette, Isler, & van Schaik, 2013). Hence, the mainly arboreal orang-utans would maintain their social bonds through other mechanisms than those of the African apes. Moreover, orang-utans do not need to maintain strong social bonds due to the extreme rarity of explicit cooperation, including coalitionary agonistic interactions (see Marzec et al., 2016).

An important issue that we are not able to resolve with the current data is that infants were not themselves in charge of being in an association or not, but could often choose to make use of it, unless their mother prevented them. To investigate the active choice of interactions and partners, we intend to look more closely at the specific initiation of interactions and the communicative behaviours involved. Throughout an infant's

development, association types are highly variable: while the time spent with female associates is constant over the age of the dependent offspring, the time spent with male associates increases (Mitra Setia et al., 2009; van Schaik, 1999). Another problem may be that we focused on social activities of very different duration: play usually lasted several minutes whereas the other social activities tended to be shorter than the 2 min bout interval. The risk of missing begging and gazing bouts was therefore higher than missing play bouts. In addition, once an infant plays with, gazes at or begs to one class of partner it usually cannot at the same time do this with another available partner. This might quickly lead to a bias in the social data of populations where associations are infrequent (especially at Tuanan) and begs the question of what a representative sample size is when using 2 min focal scans for these species. However, this is of course an inherent issue of all field data collection.

In sum, we found that in the semisolitary orang-utans, infants used interaction opportunities in both populations, and this use was predicted by various individual and social factors, such as age, party composition, interaction type and target. Infants of the more gregarious population at Suaq showed higher rates of social play and gazing, a direct consequence of more frequent associations with individuals. Irrespective of study population, infants' peers and siblings comprised the most important social partners for social play, while associations with unflanged males (potential 'cultural vectors' in orang-utan populations) may provide social learning opportunities. The fact that infants seem to actively use social learning opportunities when they arise thanks to the mother's willingness to associate with other mother–offspring pairs, adolescents or unflanged males suggests a profound benefit of interactional experiences for the physical and social skill set in adulthood.

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