**Social Stress as a Cost of Sociality in Wild *Pongo pygmaeus wurmbii***

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**Abstract**

Living in social groups has costs and benefits that vary among primate species. Constrained by low fruit availability, orangutans (*Pongo sp*.) are less social than other apes and are considered semi-solitary. While studies give the impression of general social aversion, orangutans in Gunung Palung National Park (GPNP) do form associations, particularly during periods of high fruit availability. To better understand the mechanisms that modulate sociality, we examined the possibility that socializing is stressful by exploring social anxiety, measured by self-directed behavior (SDB), and stress more generally, through urinary cortisol, among different age-sex classes under social and solitary conditions. Data were collected in GPNP from 1994-2009 and 2013-2014 during full-day focal follows. Urine was collected from the first morning urination and analyzed by enzyme immunoassay for cortisol (N=745). All instances of self-directed behavior (SDB), including self-scratching, yawning, and self-grooming, were recorded during ten-minute ‘SDB follows’ (N=1,534). Overall, orangutans had higher rates of SDB and cortisol when they were social than when they were alone (*t*(1331.41)=3.068, p=0.002; *t*(892)=2.501, p=0.013, respectively). GLMMs revealed that age-sex class significantly influences SDB and cortisol, with nulliparous females having the highest rates of SDB (β=0.250, p<0.001) and parous females having the highest cortisol levels (β=141,335.39, p=0.006). We found evidence that nulliparous females may serve as social buffers for one another. We discuss how the costs and benefits of socializing change over the life span in conjunction with energetic needs. We suggest that measuring SDB may be a useful tool for assessing relationship quality in wild orangutans.

**Keywords**

Ape, stress, self-directed behavior, cortisol, sociality

**Introduction**

Understanding primate sociality is a central issue in primatology. Living in social groups has costs and benefits that vary across and within species, being influenced by many factors including distribution of resources, predation pressure, and infanticide risk (Sterck *et al.* 1997; van Schaik 1999; Wrangham 1980). Orangutans (*Pongo sp*.) are unusual among higher primates in their low degree of sociality. Described as semi-solitary (Galdikas 1985a), with individual based fission-fusion dynamics (van Schaik 1999), orangutans provide a fairly unique opportunity to explore differences between social and solitary states within one population. With high levels of mating resistance (Fox 2002; Knott et al. 2008; Knott et al. 2009; Utami Atmoko et al. 2009), little affiliative social interaction among adults (van Noordwijk et al. 2012), and active avoidance among adult females (Knott et al. 2008), orangutan studies suggest general social aversion. Orangutans on Borneo are said to be even less social than their Sumatran counterparts (Mitra Setia et al. 2009; van Schaik 1999). This has been attributed to the lower fruit availability on Borneo compared to Sumatra (van Schaik 1999; Wich et al.2006; Marshallet al*.* 2009).

For an ape that spends most of its time ranging solitarily, encountering conspecifics may elicit psychological stress. Coming together is necessary, at least occasionally, for the practical reasons of mating or attraction to a rare food source. Are these and other gatherings costly? While it has been demonstrated that contest competition exists for Sumatran orangutans for access to large fig trees (Utami et al. 1997a), and females on Borneo avoid one another due to scramble competition within their highly overlapping ranges (Knott et al. 2008), social encounters and agonistic encounters are rare overall (Knott et al. 2008; Utami Atmoko et al. 1997b). What, then, is the proximate mechanism that keeps orangutans away from one another more generally? This study aims to examine the possibility that stress is experienced under social conditions, thereby deterring orangutans from associating more frequently than is necessary. This study explores stress in this wild population in two different non-invasive ways – by measuring the stress hormone cortisol in urine and by looking at anxiety as measured by self-directed behavior (SDB).

Stress, as an adaptive response, should signal the need for a change in behavior, as well as physiology. Thus, measuring stress can be a useful way to examine how adaptive behaviors emerge. Cortisol is an adrenal steroid hormone and plays a large role in the stress response. The catabolic effects of cortisol mobilize resources for the central nervous system, cardiovascular system, and skeletal muscles when faced with fitness-compromising situations. Chronically elevated levels of cortisol can have detrimental effects on health, reproduction and survival (Bercovitch and Ziegler 2002; Creel 2001; Sapolsky 2005; Wasser et al. 2000). As such, cortisol has been studied in many primates as a non-invasive way of measuring the costs associated with various social factors including social rank (Schoof and Jack 2013; Sapolsky 2005; Kahlenberg et al.2008), received aggression (Surbeck et al. 2012), and the threat of infanticide (Engh et al. 2006). Captive Bornean orangutans have been found to display a greater stress response to being housed in larger social groups in zoos than Sumatran orangutans (Weingrill et al. 2011). If Bornean orangutans are socially stressed by large social groups in captivity, under non-nutritionally stressed conditions, it seems possible that they are inherently socially averse. As such, we expect to find elevated cortisol levels after socializing.

Anxiety, a subset of stress, is an emotional state of uneasiness or tension in response to a situation that may pose a threat (Maestripieri et al. 1992). Self-directed behavior is an indicator of social anxiety (Aureli and Yates 2010; Castles e al. 1999; Kutsukake 2003). Self-directed behavior (SDB) most commonly includes yawning, scratching, and autogrooming and has been used widely as a way of assessing anxiety across the order Primates, including in strepsirrhines (Castles et al.1999; Manson and Perry 2000; Palagi and Norscia 2011; Polizzi di Sorrentino et al. 2012; Schino et al. 1996; Watson et al. 1999), catarrhine and platyrrhine monkeys (Schino et al.1996 in macaques; Castles et al.1999 in olive baboons; Manson and Perry 2000 in white-faced capuchins; Polizzi di Sorrentino et al*.* 2012 in capuchins), and also in apes (Kutsukake 2003; Peel et al. 2005) and humans (Troisi 2002). Rates of SDB are decreased and increased, respectively, by anxiolytic and anxiogenic drugs, which supports the use of SDB as a behavioral marker of anxiety (Polizzi di Sorrentino et al. 2012; Schino et al. 1996).

We hypothesize that socializing is stressful for orangutans. Based on the higher energetic requirements of parous females and flanged males compared to adolescent females and unflanged males, we also hypothesize that these classes suffer greater costs from socializing. Lactation is the most costly component of mothering (Clutton-Brock et al. 1989; Gittleman and Thompson 1988; Thompson 2013; Emery Thompson et al. 2012), as milk production is energetically expensive, which can be associated with elevated cortisol levels during periods of limited food availability (Emery Thompson et al. 2010). Captive lactating female orangutans were found to have elevated levels of fecal glucocorticoid concentrations compared to non-lactating and juvenile females (Weingrill et al. 2011). We also expect social partners of larger body size to be more costly than others because they present a higher degree of foraging competition and also pose a higher risk of aggression. As such, we predict that a) compared to solitary activity, socializing with at least one other individual is associated with increased cortisol levels and higher rates of SDB, b) socializing is associated with a greater increase in cortisol and in SDB for adult females and flanged males compared to adolescent females and unflanged males, c) socializing with adult female and flanged male social partners will be associated with higher rates of self-directed behavior for each age-sex class.

**Methods**

*Study Period*

Data collection took place over two different periods. From 1994-2002 and in 2009, social data along with urine samples for cortisol were collected as part of a long-term orangutan study in Gunung Palung. From July 2013-July 2014 self-directed behavior and social data were collected. The current study uses temporally distinct datasets for SDB and cortisol. We examine the social contexts of both measures to determine if they are influenced by the same factors and are, therefore, likely to be associated in orangutans.

*Study Site*

Gunung Palung National Park is located in West Kalimantan, Indonesia on the island of Borneo. It is a 108,000-hectare park that includes one of the few remaining areas of primary lowland mixed Dipterocarp forest on Borneo. Within the park is Cabang Panti Research Station (1130 S, 11070 E), which covers 2,100 hectares and contains a system of trails formed from transects. Seven different habitat types have been identified here, including peat swamp, alluvial bench, freshwater swamp, lowland sandstone, lowland granite, upland granite, and montane forest (Marshall et al. 2014). Logging has taken place periodically within and adjacent to the park since the 1960s (Johnson et al. 2005). Although legal logging concessions were closed over 30 years ago (Johnson et al. 2005), illegal hand-logging continues today. The interior of the park and Cabang Panti Research station remain largely undisturbed (Marshall et al. 2009).

*Study Population*

The orangutans in Gunung Palung are members ofthe subspecies *Pongo pygmaeus wurmbii.* The age-sex class designations used here include adolescent females, adult females, unflanged males, and flanged males. Adolescent females are defined here as young, nulliparous females that spend over 50% of their time away (more than 50 meters) from their mother. Adolescent females are nutritionally independent, are smaller than adult females, and spend the majority of their time ranging alone or in the company of individuals that are not their mother.

From 1994-2002, and in 2009, 44 individuals were followed and had urinary cortisol samples taken: 6 adolescent females, 15 adult females, 14 flanged males, and 9 unflanged males During 2013-2014, 33 individuals were sampled: 8 adolescent females, 12 adult females, 7 flanged males, and 6 unflanged males were followed and used for SDB analyses.

Females are considered to be adult once they are pregnant for the first time. Adult female orangutans almost always have an infant or juvenile offspring that ranges with them, sleeps in their nest, and nurses from them. Sexually mature male orangutans come in two distinct forms (Utami Atmoko and Van Hooff 2004). Unflanged males are independently ranging, and are not known to associate with their mother. They lack the fatty cheek pads and throat sacs that flanged males display, and are smaller than flanged males in body size.

*Behavioral Data*

Data collection period 1994-2002, 2009: All occurrences and durations of associations were recorded continuously during full-day focal follows, where the orangutan was followed from waking in their sleeping nest in the morning until falling asleep in their new nest that evening.

Data collection period 2013-2014: Ten-minute periods of dedicated ‘SDB follows’ were conducted (N=1,533 SDB follows) during full-day focal follows. SDB rates were recorded for adolescent females (N=353, 190 were social), 498 for adult females (188 were social), 407 for flanged males (179 were social), and 275 for unflanged males (224 were social).

To avoid under-counting the true occurrence of SDBs which could take place when individuals are out of view even for a just a few seconds, ten-minute focused ‘SDB follows’ were conducted as often as possible (with a mean of 15 per follow) throughout focal follows, ensuring that the observer’s gaze was never averted from the focal animal and all instances of self-scratching, yawning, and self-grooming were accurately recorded. SDB rates were defined as the number of self-directed behaviors performed per ten minutes. As many SDB follows as possible were carried out over the course of a day, attempting to sample multiple individuals when possible during a social event. Effort was made to sample each individual under both social and non-social conditions. For every SDB follow, it was noted whether or not a conspecific was within 50 meters of the focal, deeming that period as social or solitary. A self-scratch was defined as “raking one’s own hair or skin with fingernails” (Baker and Aureli 1997). Self-grooming was defined as picking at or removing something from the skin or hair or moving the hair and inspecting the skin as if looking to remove something. Yawning was defined as opening one’s mouth widely and inhaling deeply. SDB follows that were performed during obvious scratch-inducing events, such as eating *Neesia* fruits (with their many tiny irritant hairs), an attack by a swarm of bees, or getting covered in many termites, were aborted and excluded from analysis.

*Urine Collection and Urine Analysis*

Urine samples were collected in Gunung Palung National Park from 1994-2002 and also in 2009, and dried on filter paper, following established protocols (Knott 1997). The samples were analyzed in the Hominoid Reproductive Ecology laboratory at the University of New Mexico using competitive enzyme-immunoassay (EIA). Intrassay CV for replicate aliquots of the same sample was 7.1% (N =7). All steroid concentrations were standardized for creatinine concentration to control for water content (Taussky and Kurzmann 1954), and overly dilute samples (Cr < 0.05 mg/ml) were excluded due to the tendency for this to over-inflate steroid estimates.

To account for diurnal variation of cortisol secretion (Anestis and Bribiescas 2004), with levels highest in the morning and lowest at night, we only used first morning urine samples, collected when the orangutan first emerged from the night nest. Orangutan wake time can sometimes vary by many hours, so we also excluded any samples collected after 12:00, even if it appeared to be the first urination of the day. Cortisol outliers (defined as values that were more than two standard deviations above or below the average cortisol level) were calculated for each age-sex class and excluded from analysis. Only samples collected the morning after full-day follows that were at least 360 minutes long were included in this analysis to ensure that it was known whether a social event had taken place the day prior. Urine samples from infants/juveniles and overtly sick or injured individuals were excluded from this dataset. A total of 738 samples were used for data analysis in the current study, with 80 samples from adolescent females, 415 from adult females, 226 from flanged males, and 18 from unflanged males.

*Caloric Intake*

It has been suggested that orangutans may congregate when they are least food stressed, but also may be forced to come together at a rare food source when conditions are poor (Sugardjito 1987). Cortisol can be elevated as a result of both psychosocial and physical/nutritional stress (Whitten et al. 1998), which can complicate our understanding of the causes of increased cortisol measures. Therefore, we controlled for caloric intake the day before a urine sample was collected as a factor that may influence cortisol concentration in urine. Kilocalories consumed per day were estimated via standard methods (Knott 1998; Harrison *et al.* 2010).

*Cortisol Analysis*

General linear mixed models (GLMM) in SPSS were used to predict cortisol levels, using each sample, and its corresponding follow from the previous day, as the unit of analysis. Cortisol values were square root transformed in order to approach normality and meet the assumptions of the GLMM. Different models were fitted using the factors focal age-sex class, social state (social or solitary), and kilocalories consumed. Kilocalories consumed the day before urine collection was used as a predictor because it is expected that nutritional status influences cortisol levels (Emery Thompson 2017; Emery Thompson et al. 2010; Whitten et al. 1998). The presence or absence of social partners of each age-sex class were not included as predictors in these models because there was insufficient data within each of those conditions. Models were run using each of the factors separately and in all possible combinations, with and without interaction effects. Focal ID was used as a random factor in each model. Akaike’s Information Criterion was used to determine the model of best fit.

*Self-directed behavior*

GLMMs in SPSS were used to predict SDB rate, using each 10-minute SDB follow as the unit of analysis. A Poisson distribution model was used to accommodate count data (number of SDBs per ten-minute increment) as the target. Different models were fitted using the factors of focal age-sex class and social state (social or solitary). Models were run using each factor separately, and in all possible combinations, with and without interaction effects. Orangutan ID was used as a random factor in each model. Akaike’s Information Criterion was used to determine the model of best fit.

Using the parameters of the best-fit model, we also ran models to examine the effect of the presence or absence of social partners of each age-sex class on the rate of self-directed behavior. For instance, does socializing with a flanged male induce more anxiety for an adult female than socializing with an adolescent female? We ran a separate model for each age-sex class of the social partner with focal age-sex, social state, their interaction, the presence or absence of a given age-sex class social partner, and the three-way interaction of focal age-sex, social state, and the presence or absence of a given age-sex social partner. Focal orangutan ID was used as a random factor in each model.

*Ethical Note*

This research complied with the protocols approved by the Institutional Animal Care and Use Committee of Boston University (protocol 08-037). This research was approved by the State Ministry of Research and Technology of Indonesia (permit number 194/SIPFRP/SM/VI/2013). Our research methods were non-invasive and did not endanger the welfare of our study subjects.

**Results**

*Urinary Cortisol Concentration*

In assessing the factors that influence cortisol concentration in urine, multiple models were compared using AICc to adjust for small sample size. In the best fit GLMM (based on AICc of 9008.65), age-sex, social state, kcals consumed, and the interaction between age-sex and social state were used as fixed effects. Age-sex class had a significant influence on urinary cortisol concentration (β=155.11, F=6.335, p<0.001, Table 1). Adult females had significantly higher cortisol than all other age-sex classes (compared to adolescent females: *t*(708)=2.907, p=0.004; compared to flanged males: *t*(708)=2.738, p=0.006; compared to unflanged males: *t*(708)=2.547, p=0.011) (Figure 1).

We predicted that larger classes of focal individuals would experience a greater increase in cortisol during social versus non-social conditions. While the parameter estimate of this overall interaction effect (age-sex \* social state) was not significant, including it did substantially improve the model fit (ΔAICc= -30.77). When the interaction effect was omitted, the main effect of social state on cortisol was significant (β=31.68, F=6.892, p=0.009), such that social contexts elicited higher cortisol. In the full model with interaction, our specific prediction was upheld by pairwise comparisons: adult females and flanged males had significantly elevated cortisol under social conditions compared to solitary conditions (adult female: *t*(708)=2.266, p=0.024; flanged male: *t*(708)=2.099, p=0.036) (Figure 2). By contrast, adolescent females and unflanged males did not have significantly different cortisol under social and non-social conditions (p=0.754, p=0.990, respectively).

**Table 1. Fixed effects of the GLMM predicting urinary cortisol concentration based on the effect of focal age-sex, social state (social, Y or solitary, N), the interaction between them, and kilocalories consumed the day prior to sample collection. Significant effects (<0.05) are in bold.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **F** | ***df1*** | ***df2*** | **P** |
| Corrected Model | 3.510 | 8 | 708 | 0.001 |
| Focal age-sex | 6.335 | 3 | 708 | **0.000** |
| Social Y or N | 0.896 | 1 | 708 | 0.344 |
| Kcal consumed | 0.166 | 1 | 708 | 0.684 |
| Focal age-sex\*Social Y or N | 0.920 | 3 | 708 | 0.431 |

**

**Figure 1. Urinary cortisol concentration for each age-sex class as predicted by age-sex, social state, their interaction, and kilocalories consumed the day prior to urine sample collection. There are significant differences among the age-sex classes in urinary cortisol concentration, adult females have significantly higher cortisol compared to all other age-sex classes (adolescent females, P<0.001; flanged males, p=0.021; unflanged males, p=0.003).**



**Figure 2. Mean cortisol of each age-sex class when they are social versus solitary. Socializing is associated with a significant increase in cortisol in adult females (p=0.024) and flanged males (p=0.036). Socializing does not significantly influence urinary cortisol for adolescent females or unflanged males.**

*Self-Directed Behavior*

Self-directed behavior was predicted by an interaction of focal age-sex and social state (F1,525=3.072, p=0.027) (Table 2). Figure 3). This effect was drive by adolescent females who had an overall higher rate of scratching than other individuals While rates of DSB increased in social contexts for adolescent females (t(1,525)=2.873, p=0.004), rates of SDB were not significantly different between social and solitary contexts for the other age-sex classes (Figure 5).

**Table 2. Results of a GLMM predicting rate of self-directed behavior based on the effect of focal age-sex, social state (social or solitary), and the interaction between focal age-sex and social state on rate of self-directed behavior in wild orangutans.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **F** | ***df1*** | ***df2*** | **P** |
| Corrected Model | 6.209 | 7 | 1,525 | 0.000 |
| Focal age-sex | 3.250 | 3 | 1,525 | 0.021 |
| Social state | 5.286 | 1 | 1,525 | 0.022 |
| Focal age–sex \*Social state | 3.072 | 3 | 1,525 | 0.027 |

****

**Figure 3. Rate of self-directed behavior is significantly higher when social compared to when solitary, controlling for age-sex class and the interaction between age-class and social yes or no (p=0.025).**



**Figure 4. Rate of self-directed behavior for each age-sex class when controlling for their social state and the interaction between their age-sex class and their social state. Adolescent female rate of self-directed behavior is significantly higher than each of the other age-sex classes in pairwise comparisons (p=0.033 compared to adult females; p=0.045 compared to flanged males; p=0.040 compared to unflanged males) while no other differences between age-sex classes were significant.**

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**Figure 5. Mean rate of self-directed behavior among the age-sex classes under social and solitary conditions. Rate of self-directed behavior is significantly different between the social states for adolescent females only (p=0.003)**

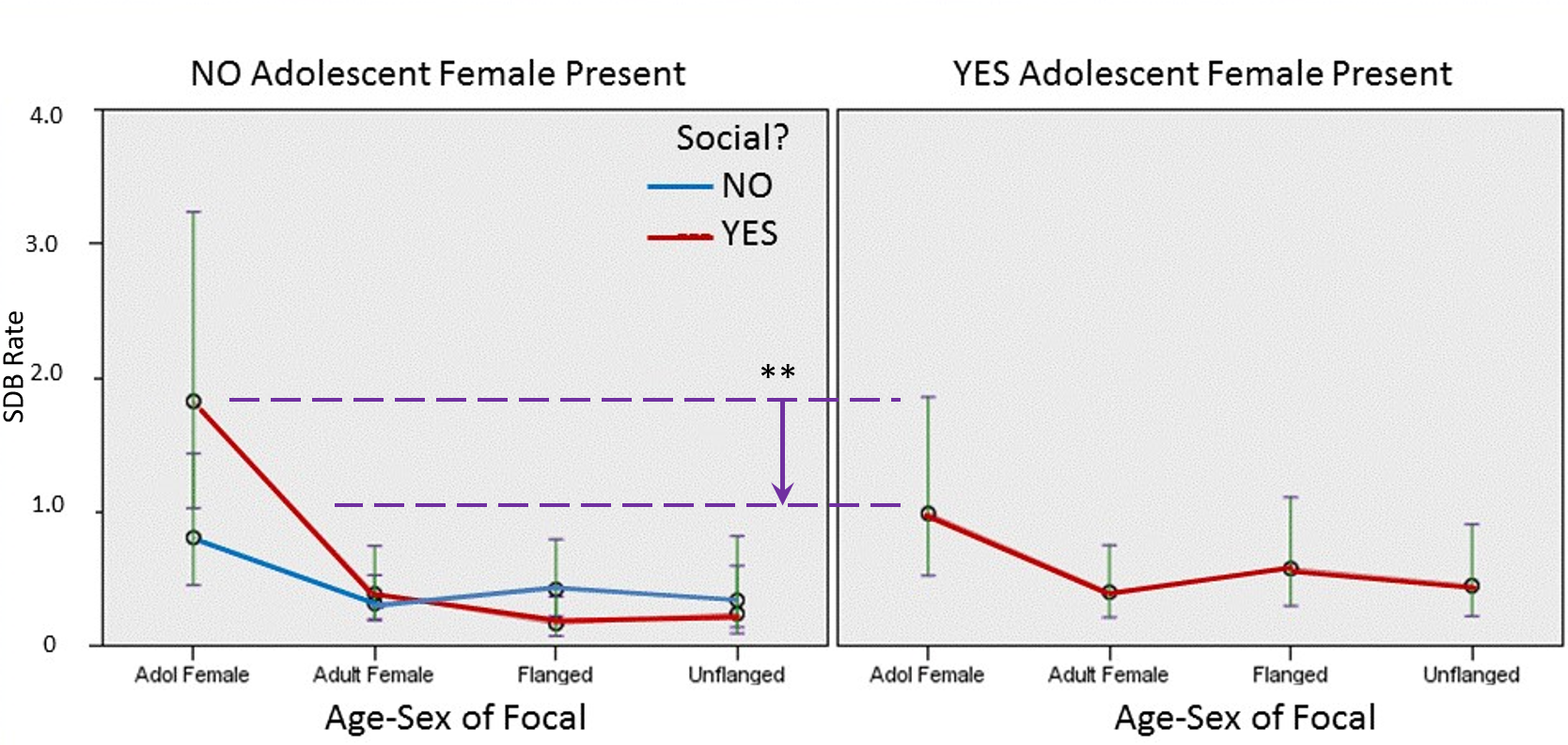
We evaluated a series of additional models including interaction effects for the presence or absence For an adolescent female focal, being social with another adolescent female is associated with a significantly lower rate (mean 0.991±0.317) of self-directed behavior than being social with other age-sex classes (mean 1.826+0.532) (β=1.23, F=8.943, p<0.001) (Table 3) (Figure 6). Flanged male focals have significantly higher mean rates of SDB when social with adolescent females (0.581±0.192) compared to when they are social with other age-sex classes (0.171±0.068) (p<0.01). No other three-way interactions were significant – in other words, socializing with adolescent females has no significant influence on rate of SDB for adult females or unflanged males (Table 4).

**Table 3. Results of a GLMM predicting rate of SDB based on the effect of focal age-sex, social state (social or solitary), interaction between them, the presence or absence of an adolescent female social partner, and the three-way interaction between the age-sex of the focal\*Social state\*presence or absence of an adolescent female social partner. Significant effects are in bold.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **F** | ***df1*** | ***df2*** | **P** |
| Corrected Model | 6.686 | 11 | 1,521 | 0.000 |
| **Focal age-sex** | 3.871 | 3 | 1,521 | **0.009** |
| Social Y or N | 0.137 | 1 | 1,521 | 0.711 |
| **Focal age-sex\*Social Y or N** | 3.332 | 3 | 1,521 | **0.019** |
| Adolescent Female Present Y or N | 3.443 | 1 | 1,521 | 0.064 |
| **Focal age-sex\*Social Y or N\*Adolescent Female Present Y or N** | 8.943 | 3 | 1,521 | **0.000** |

**Table 4. Pairwise contrasts between an adolescent female social partner not present versus present for each focal age-sex class when social. Significant contrasts are in bold.**

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Focal age-sex** | **Social Y/N** | **Adol Female Present Y or N** | **Cont. Est.** | **Std. Err.** | ***t*** | ***df*** | **Adj. Sig.** | **Low CI (95%)** | **Upp CI (95%)** |
| Adol Female | Y | N-Y | 0.835 | 0.353 | 2.363 | 1,521 | **0.018** | 0.142 | 1.528 |
| Y-N | -0.835 | 0.353 | -2.363 | 1,521 | **0.018** | -1.528 | -0.142 |
| Adult Female | Y | N-Y | -0.014 | 0.147 | -0.094 | 1,521 | 0.925 | -0.303 | 0.275 |
| Y-N | 0.014 | 0.147 | 0.094 | 1,521 | 0.925 | -0.275 | 0.303 |
| Flanged Male | Y | N-Y | -0.410 | 0.155 | -2.643 | 1,521 | **0.008** | -0.714 | -0.106 |
| Y-N | 0.410 | 0.155 | 2.643 | 1,521 | **0.008** | 0.106 | 0.714 |
| Unfl.  Male | Y | N-Y | -0.209 | 0.150 | -1.394 | 1,521 | 0.164 | -0.504 | 0.085 |
| Y-N | 0.209 | 0.150 | 1.394 | 1,521 | 0.164 | -0.085 | 0.504 |



**Figure 6. The effect on SDB rate of the three-way interaction among the age-sex class of the focal, whether or not the focal is social, and the presence or absence of an adolescent female social partner. The significant decrease in rate of SDB (p=0.012) for adolescent female focals when they are social with another adolescent female is indicated by the purple dotted lines and arrow.**

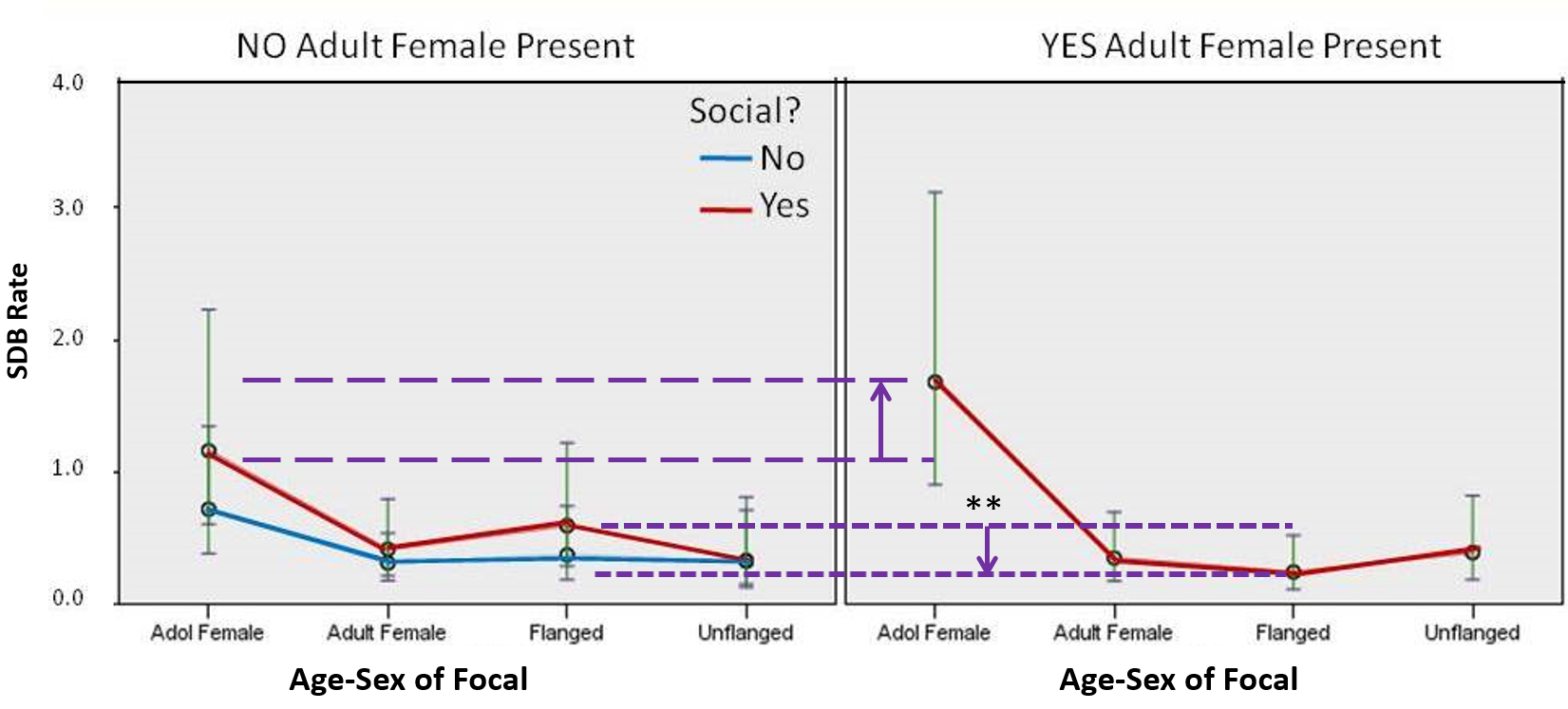
The presence or absence of an adult female social partner does not have a significant effect on rate of self-directed behavior on its own (β=0.164, F=0.939, p=0.333), however, the three-way interaction among age-sex of focal, social state, and the presence or absence of an adult female was a significant predictor of rate of self-directed behavior (β=1.043, F=5.547, p=0.001) (Table 5). For an adolescent female focal, being social with an adult female is associated with a higher rate (mean 1.681±0.528) of self-directed behavior than being social with other age-sex classes (mean 1.164±0.385), although this difference did not quite reach significance (p=0.055) (Figure 7). Flanged male focals have significantly lower mean rate of SDB when social with adult females (0.248±0.095) compared to when they are social with other age-sex classes (0.598 ±0.218) (p<0.05). No other three-way interactions were significant – in other words, socializing with adult females has no significant influence on rate of SDB for other adult females or for unflanged males (Table 6).

**Table 5 Results of a GLMM predicting rate of SDB based on the effect of focal age-sex, social state (social or solitary), interaction between them, the presence or absence of an adult female social partner, and the three-way interaction between the age-sex of the focal\*social state\*presence or absence of an adult female social partner. Significant effects are in bold.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **F** | ***df1*** | ***df2*** | **P** |
| Corrected Model | 5.609 | 11 | 1,521 | **0.000** |
| Focal age-sex | 3.018 | 3 | 1,521 | **0.029** |
| Social Y or N | 5.665 | 1 | 1,521 | **0.017** |
| Adult Female Present Y or N | 0.939 | 1 | 1,521 | 0.333 |
| Focal age-sex\*Social Y or N | 3.179 | 3 | 1,521 | **0.023** |
| Focal age-sex\*Social Y or N\*Adult Female Present Y or N | 5.547 | 3 | 1,521 | **0.001** |

**Table 6. Pairwise contrasts between an adult female social partner not present versus present for each focal age-sex class when social. Significant contrasts are in bold.**

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Focal age-sex** | **Social**  **Y/N** | **Adult Female Present Y or N** | **Cont. Est.** | **Std. Err.** | ***t*** | ***df*** | **Adj. Sig.** | **Low**  **CI**  **(95%)** | **Upp.**  **CI (95%)** |
| Adol Female | Y | N-Y | -0.516 | 0.269 | -1.919 | 1,521 | 0.055 | -1.044 | 0.011 |
| Y-N | 0.516 | 0.269 | 1.919 | 1,521 | 0.055 | -0.011 | 1.044 |
| Adult Female | Y | N-Y | 0.066 | 0.139 | 0.472 | 1,521 | 0.637 | -0.208 | 0.339 |
| Y-N | -0.066 | 0.139 | -0.472 | 1,521 | 0.637 | -0.339 | 0.208 |
| Flanged Male | Y | N-Y | 0.350 | 0.160 | 2.183 | 1,521 | **0.029** | 0.036 | 0.664 |
| Y-N | -0.350 | 0.160 | -2.183 | 1,521 | **0.029** | -0.664 | -0.036 |
| Unfl.  Male | Y | N-Y | -0.060 | 0.091 | -0.661 | 1,521 | 0.509 | -0.238 | 0.118 |
| Y-N | 0.060 | 0.091 | 0.066 | 1,521 | 0.509 | -0.118 | 0.238 |



**Figure 7. The effect on SDB rate of the three-way interaction among the age-sex class of the focal, whether or not the focal is social, and the presence or absence of an adult female social partner. The significant decrease in rate of SDB (p=0.004) for flanged male focals when they are social with adult females is indicated by the purple dotted lines and arrow. The increase in rate of SDB for adolescent female focals when they are social with adult females is also indicated by purple dotted lines and an up arrow**

For the model looking at the effect of the presence or absence of a flanged male social partner, the presence of a flanged male social partner has a significant effect on rate of self-directed behavior (β= 0.084, F=10.389, p=0.001) (Table 7), elevating the rate of self-directed behavior for adolescent females significantly from a mean of 1.32±0.39 scratches per 10 minutes when they socialize with adult females, unflanged males, or other adolescent females to 2.21±0.69 when they socialize with flanged males (p=0.019) (Table 8, Figure 8). A flanged male social partner had no significant effect on the adult female rate of self-directed behavior (Table 8), and, due to the rarity of social events between adult males, there were no data for flanged or unflanged male focals for this social condition.

**Table 7. Results of a GLMM predicting rate of SDB based on the effect of focal age-sex, social state (social or solitary), interaction between them, the presence or absence of a flanged male social partner, and the three-way interaction between the age-sex of the focal\*social state\*presence or absence of a flanged male social partner. Significant effects are in bold.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **F** | ***df1*** | ***df2*** | **P** |
| Corrected Model | 7.512 | 9 | 1,523 | 0.000 |
| **Focal age-sex** | 3.785 | 3 | 1,523 | **0.010** |
| Social Y or N | 1.801 | 11 | 1,523 | 0.180 |
| Focal age-sex\*Social Y or N | 1.984 | 3 | 1,523 | 0.114 |
| **Flanged Male Present Y or N** | 10.389 | 1 | 1,523 | **0.001** |
| Focal age-sex\*Social Y or N\*Flanged Male Present Y or N | 0.059 | 1 | 1,523 | 0.808 |

**Table 8. Pairwise contrasts between a flanged male social partner *not* present versus present for each focal age-sex class when social. Significant contrasts (<0.05) are in bold. The data set contained no instances of flanged males associating with other males.**

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Focal age-sex** | **Social Y/N** | **Flanged Male Present Y or N** | **Cont. Est.** | **Std. Err.** | ***T*** | ***df*** | **Adj. Sig.** | **Low.**  **CI (95%)** | **Upp.**  **CI (95%)** |
| Adol Female | Y | N-Y | -0.890 | 0.378 | -2.355 | 1,523 | **0.019** | -1.631 | -0.149 |
| Y-N | 0.890 | 0.378 | 2.355 | 1,523 | **0.019** | 0.149 | 1.631 |
| Adult Female | Y | N-Y | -0.250 | 0.155 | -1.620 | 1,523 | 0.105 | -0.053 | 0.053 |
| Y-N | 0.250 | 0.155 | 1.620 | 1,523 | 0.105 | -0.053 | 0.553 |



**Figure 8. The effect of the three-way interaction among the age-sex class of the focal, whether or not the focal is social, and the presence or absence of a flanged male social partner on the rate of SDB of the focal. There is a significant increase in rate of SDB (p=0.019) for adolescent female focals when they are social with flanged males compared to when they are social with other age-sex classes.**

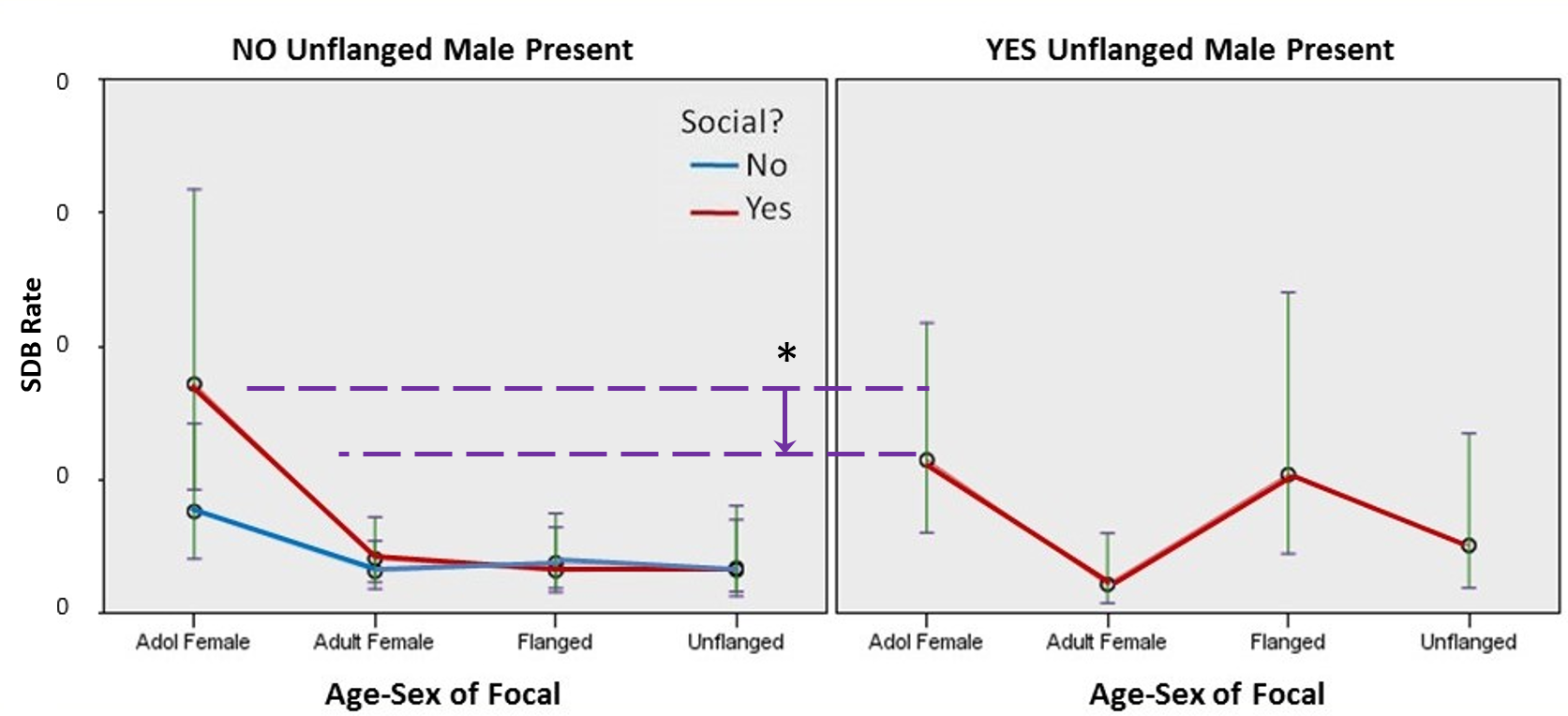
The presence or absence of an unflanged male social partner did not significantly contribute to the model on its own (p=0.451) (Table 9). However, the three-way interaction of focal age-sex, social state, and the presence or absence of an unflanged male social partner does significantly influence the rate of SDB (β=0.401, F=7.505, p<0.001, Table 9). More specifically, for an adolescent female focal, socializing with an unflanged male is associated with a significantly lower rate of SDB (mean 1.150±0.374) than socializing with other age-sex classes (mean 1.717±0.537) (p=0.030) (Table 10, Figure 9). No other age-sex classes’ rate of self-directed behavior were significantly affected by the presence or absence of an unflanged male (Table 10).

**Table 9. Results of a GLMM predicting rate of SDB based on the effect of focal age-sex, social state (social or solitary), interaction between them, the presence or absence of an unflanged male social partner, and the three-way interaction between the age-sex of the focal\*social state\*presence or absence of an unflanged male social partner. Significant effects (<0.05) are in bold.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **F** | ***df1*** | ***df2*** | **P** |
| Corrected Model | 6.288 | 11 | 1,521 | 0.000 |
| Focal age-sex | 3.283 | 3 | 1,521 | **0.020** |
| Social Y or N | 3.904 | 1 | 1,521 | **0.048** |
| Focal age-sex\*Social Y or N | 1.659 | 3 | 1,521 | 0.174 |
| Unflanged Male Present Y or N | 0.567 | 1 | 1,521 | 0.451 |
| Focal age-sex\*Social Y or N\*Unflanged Male Present Y or N | 7.505 | 3 | 1,521 | **0.000** |

**Table 10. Pairwise contrasts between an unflanged male social partner *not* present versus present for each focal age-sex class when social. Significant contrasts (<0.05) are in bold.**

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Focal age-sex** | **Social Y/N** | **Unfl.**  **Male Present Y or N** | **Cont.**  **Est.** | **Std. Err.** | ***t*** | ***df*** | **Adj. Sig.** | **Low.**  **CI**  **(95%)** | **Upp. CI (95%)** |
| Adol Female | Y | N-Y | 0.567 | 0.262 | 2.168 | 1,521 | **0.030** | 0.054 | 1.080 |
| Y-N | -0.567 | 0.262 | -2.168 | 1,521 | **0.030** | -1.080 | -0.054 |
| Adult Female | Y | N-Y | 0.192 | 0.123 | 1.570 | 1,521 | 0.117 | -0.048 | 0.433 |
| Y-N | -0.192 | 0.123 | -1.570 | 1,521 | 0.117 | -0.433 | 0.048 |
| Flanged Male | Y | N-Y | -0.718 | 0.376 | -1.909 | 1,521 | 0.056 | -1.456 | 0.020 |
| Y-N | 0.718 | 0.376 | 1.909 | 1,521 | 0.056 | -0.020 | 1.456 |
| Unfl. Male | Y | N-Y | -0.169 | 0.212 | -0.797 | 1,521 | 0.425 | -0.586 | 0.247 |
| Y-N | 0.169 | 0.212 | 0.797 | 1,521 | 0.425 | -0.247 | 0.586 |



**Figure 9.** **The effect on SDB rate of the three-way interaction among the age-sex class of the focal, whether or not the focal is social, and the presence or absence of an unflanged male social partner. The significant decrease in rate of SDB (p<0.05) for adolescent female focals when they are social with unflanged males is indicated by the purple dotted lines and down arrow**

**Discussion**

*Cortisol*

Socializing is associated with an increase in cortisol concentration in the Gunung Palung orangutan population. Being the most social age-sex class and having the highest average rate of self-directed behavior, it might be expected that adolescent females should have high levels of cortisol. However, adult females have the highest cortisol levels of all age-sex classes and adolescent females have relatively moderate levels. These findings may be explained by the connection between cortisol and energetic stress. Adult females have the added energetic burden of motherhood compared to the other age-sex classes, having to carry their babies as they travel through the canopy (Knott 2004) and produce milk to sustain their offspring (Clutton-Brock et al. 1989; Gittleman and Thompson 1988; Emery Thompson 2013; Emery Thompson et al. 2012). Adult females with offspring are more energetically constrained than non-lactating nulliparous females, which may mask any social effects on cortisol levels in adolescent females in our dataset. This also may help explain the reduced tendency of adult females to socialize compared to younger, nulliparous females (O’Connell, 2018; O’Connell & Knott, 2015, 2018). It has been argued that sociality is less costly for adolescent females than for adults because of their smaller body size, long day ranges, and ease of travel (Galdikas 1995). These young females likely benefit from socializing due to the opportunities it provides for observing the ranging and social behavior of others, locating food patches via more experienced adults, protection from “enemies”, and affiliative bonds (Galdikas 1995). Unflanged males had the lowest urinary cortisol concentration of all age-sex classes. This finding is consistent with previous findings that unflanged males had lower cortisol than developing males and flanged males in captivity(Maggioncalda et al. 2002).

*Self-directed behavior*

Being social is associated with higher levels of anxiety compared to solitary conditions in orangutans in Gunung Palung National Park. Adolescent females appear particularly anxious when socializing compared to others, as indicated by their high rates of self-directed behavior even while alone. Socializing with flanged males or adult females, in particular, elicits anxiety in this age-sex class. Adolescent females are the most social age-sex class (Galdikas 1985a, 1995) and they seek and maintain social associations more regularly than other age-sex classes (O’Connell, 2018; O’Connell & Knott, 2018). Adolescent females must gain meaningful benefits from associating with flanged males and adult females in order to overcome the cost of anxiety that these groupings are associated with. Interestingly, socializing with another adolescent female seems to reduce anxiety for adolescent females. In this data set, when adolescent females were in association with another adolescent female, there was almost always (96% of time) an additional orangutan present. It appears that adolescent females may serve as social buffers for one another, making associating with other conspecifics less anxiety-inducing. Some have argued that indirect social support (the mere presence of kin in social groups) can reduce stress as measured through fecal glucocorticoids (Scheiber et al. 2005). Cheney and Seyfarth (2009) have argued that it is the quality of social bonds that reduces stress in female monkeys, rather than sociality itself. Orangutans display relatively few overt affiliative behaviors and almost never show coalitionary behavior (Marzec et al. 2016), so the support that nulliparous females provide one another appears to be subtle and indirect. Associating with a peer crowd has been found to be protective against feelings of social anxiety in human adolescents (Greca and Harrison 2005) and the same appears to be true for orangutans. For this study, we were able to sample only one male that we knew to be adolescent so it is not clear if male adolescent orangutans might also benefit from associating with age-mates when social with others.

Parallel dispersal occurs in many species (Schoof et al. 2009), easing the transition to a new social landscape and offering ‘safety in numbers.’ Male coalitionary behavior is the best predictor of parallel dispersal (Schoof et al. 2009), however, and male coalitions are absent in orangutans. From limited observations of the single known adolescent male observed in this study period, along with additional observations of two suspected adolescent males (it is difficult to know the age of unflanged males if they are new to the research area), it seems that they spend most of their social time with adolescent or adult females. Galdikas (1985b) has reported that ‘subadult’ males (unflanged males, which would include both adolescent and older adult unflanged males) are rather social in general but that it is mostly with females. Future observations of known young males that are observed as they achieve ranging independence will help to shed light on the nature of adolescent male orangutan social behavior.

The rate of self-directed behavior in adolescent females was also significantly reduced when they associated with an unflanged male compared to socializing with other age-sex classes. Adolescent female-unflanged male relationships are often highly affiliative (O’Connell, 2018; O’Connell & Knott, 2018). Adolescent females’ low levels of anxious behavior when in association with unflanged males lends additional support to the idea that close affiliative associations with unflanged males may have fitness benefits for adolescent female orangutans, or at the very least, come at a lower cost than associating with adult females or flanged males.

Orangutans are so often ranging alone that it is difficult to get an accurate picture of the social dynamics of a study population. Self-directed behavior may be a useful way to assess the quality of dyadic relationships and may be helpful in aiding our understanding of these socially cryptic apes. Researchers have suggested that self-directed behavior can represent “tension” in dyadic relationships and provide a means of quantifying relationship quality (Silk et al. 2013). A growing body of literature shows that social bonds have fitness consequences (Cameron et al. 2009; Schülke et al. 2010; Silk et al. 2003; Silk et al. 2013), and quantifying the nature of social relationships offers an analytical tool for understanding the evolution of social behavior. With low frequency of social interaction, few orangutan studies have attempted to examine the nature of social relationships, and simply document the occurrence of social associations to report rates of association and the basic categories of encounters including feeding aggregations, consortships, travel bands, aggressive encounters, and offspring play associations (Mitani et al. 1991; van Noordwijk et al. 2012). Research on wild orangutan behavior has yet to include self-directed behavior as a regular part of data collection, although several studies on captive orangutans have explored this (Amrein et al. 2014; Elder and Menzel 2001). Quantifying the characteristics of social relationships in the wild can help us begin to understand the nature of the orangutan social system and whether or not social bonds have implications for their reproductive fitness.

Uncertainty and unpredictability of the behavior of a social partner has been used to explain patterns of self-directed behavior in other species (Castles and Whiten 1998; Kutsukake 2003; Manson and Perry 2000). Adolescent female orangutans are relatively new to ranging independently and must work to establish their own relationships with the individuals they will likely encounter in their overlapping home ranges (Knott et al. 2008). Adult females are often aggressive towards adolescent females that associate with them, chasing, lunging at and occasionally swatting at them. Despite this, adolescent females persist in following adult females (O’Connell, 2018; O’Connell & Knott, 2018), albeit cautiously, displaying vigilance and the increased self-directed behavior reported here. It seems that uncertainty does likely play a role in the tension within these social encounters, but adolescent females seek them out anyway. When it comes to associating with other adolescent females, on the other hand, these young females likely have knowledge of many of their age-mates from ‘play groups’ they joined when they ranged with their mothers. Adult females relatives with similarly aged offspring often come into proximity and allow their dependents to play with other young orangutans (van Noordwijk et al. 2012). Being similarly sized and having previous knowledge of their social tendencies would reduce the degree of uncertainty and tension in these associations, thereby making them less anxiety inducing, as has been shown here through the lower rate of self-directed behavior for adolescent females when they are social with one another.

*Self-directed behavior and cortisol – are they associated?*

A number of studies have found no association between fecal glucocorticoids and self-directed behavior (Amrein et al. 2014; Elder and Menzel 2001; Ellis et al. 2011; Higham et al. 2009; Ulyan et al. 2006). Amrein et al*.* (2014) examined cortisol concentration in feces of zoo-housed Bornean orangutans and found that individuals did not have elevated rates of self-directed behavior and elevated cortisol at the same time, although on average, individuals who scratched themselves more also had higher mean cortisol levels. Elder and Menzel (2001) found no association between salivary cortisol and self-directed behavior in a captive orangutan during a computerized task, although only a single individual was involved in this study and cortisol has high levels of inter-individual variation (Del Giudice et al. 2011).

While we were unable to examine the direct association between self-directed behavior and cortisol here, we did find that they both increase across individuals under social conditions. Among the different age-sex classes, however, the patterns of self-directed behavior and cortisol were not the same. For example, adult females had the highest levels of cortisol but not the highest rate of self-directed behavior. An adult female orangutan almost always has at least one dependent offspring. The energetic cost of lactation alone is significant (Thompson et al., 2012) and carrying an infant or young juvenile adds to the burden, which likely accounts for their elevated levels of urinary cortisol compared to adolescent females. It may be that adult females do not experience anxiety - as manifested by an increase in self-directed behavior - when they are in the presence of conspecifics because they are established in the social landscape and are aware of their social standing with individuals they encounter regularly. Self-directed behavior can be an effective way to examine more acute stress, or tension, in social relationships of wild orangutans, while our results suggest that cortisol may be responding most acutely to energetic stress. Studies of chimpanzees support the conclusion that different classes of individuals may be more vulnerable to social versus energetic stressors (Emery Thompson et al. 2010). also we do not see elevations in cortisol with acute stressors that evoke SDB simply is n effectiveFuture studies should further investigate the physiological correlates of self-directed behavior in wild orangutans, and use matched self-directed behavior and cortisol data to explore whether they are associated.

*Exploring Social Bonds in Wild Orangutans*

Our finding that adolescent females may buffer one another from social anxiety raises the question of whether social bonds are important and confer fitness benefits for orangutans. It is very difficult to measure reproductive success in orangutans because they are very long-lived, with extremely long interbirth intervals, and individuals can go unfollowed by observers for years at a time. It could be helpful, then, to examine other factors that can serve as proxies for fitness, such as home range quality. Do individuals with stronger social relationships have better home range quality? Perhaps this relationship changes over the lifespan. Social bonds may be important for nulliparous females who are actively establishing their own home ranges but then become less important — or too costly —to maintain once they begin reproducing. Future exploration of these questions will help elucidate whether social bonds are adaptive for orangutans, whose sociality has often been underestimated.

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