

## RESEARCH ARTICLE

# Sociosexual behavioral patterns involving nulliparous female orangutans (*Pongo* sp.) reflect unique challenges during the adolescent period

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## Abstract

The primate adolescent period is characterized by a series of changes in physiology, behavior, and social relationships. Orangutans have the slowest life history and the longest period of dependency of all primates. As members of a semisolitary species with high levels of sexual coercion, adolescent female orangutans face a unique combination of challenges when achieving independence from their mother. This study examined the mating behavior of adolescent female orangutans and compared it with that of adult females to assess whether mating behavior reflects distinct strategies at these different points in the life cycle. Data were collected in Gunung Palung National Park on the island of Borneo over 20 years. Mating events from adolescent ( $n = 19$ ) and adult females ( $n = 26$ ) were scored and compared. Adolescent female mating events had significantly higher mating scores (indicating more proceptivity) than those of adult females ( $\beta = 1.948$ ,  $p = .001$ ). Adolescent females also engaged in elaborate sociosexual interactions with different flanged males, behaviors that were never observed during mating events of adult females. These interactions involved characteristic behavior on the part of both the adolescent females and the flanged males. Given these findings and the documentation of similar accounts of adolescent female–flanged male mating from the island of Sumatra, we propose that adolescent female orangutans display distinctive behavioral repertoires throughout the genus *Pongo* which serves to overcome male ambivalence toward nulliparous females, establish familiarity, and evaluate coercive tendencies in flanged males. We suggest that these behavioral patterns are an integral part of female social development in a female philopatric, but highly dispersed species where consistent social support is absent after ranging independence is achieved.

## KEYWORDS

adolescence, mating, proceptivity, sexual behavior, social development

## 1 | INTRODUCTION

Primates have long periods of development relative to most other mammals (Harvey & Clutton-Brock, 1985). Extended immature phases are thought to have evolved for various reasons including, ecological risk aversion (Janson & van Schaik, 1993), time for social

learning of complex ranging and foraging strategies (van Noordwijk & van Schaik, 2005), and gaining social skills to navigate a nuanced social landscape (Joffe, 1997). The specific definition of adolescence, the period after the juvenile phase but before adulthood, can vary by species or the research questions being asked, but is typically marked by the onset of puberty and culminates with successful reproduction

(Watts & Pusey, 1993). This period involves changes in hormones, body growth, new social relationships, emerging sexuality, and often dispersal from natal groups, and can, therefore, be characterized as a period of uncertainty and instability. Bogin (1994) has argued that adolescence is peculiar to our species. His argument rests largely on the fact that humans experience a more dramatic period of skeletal growth after puberty—the adolescent growth spurt—compared to other apes. Though the percentage of adult body size achieved during puberty may be variable between species, other primates also experience a period of rapid morphological, physiological, and behavioral change after the onset of puberty that makes the period before first reproduction one that is clearly distinct from both the juvenile and adult phases (Setchell & Lee, 2004).

Orangutans have the slowest life history of the great apes (van Noordwijk et al., 2018; Wich et al., 2009) with remarkably long periods of development. Young orangutans nurse from their mothers for 5 to 7 years before weaning and achieve ranging independence around the time their mother gives birth to a new baby when they are 6 to 9 years old (van Noordwijk et al., 2009). The behavioral and genetic evidence indicate that orangutans are female philopatric, with male-biased dispersal (Arora et al., 2012; Knott et al., 2008; Nietlisbach et al., 2012; van Noordwijk et al., 2012) as would be predicted for nongregarious primates (Kappeler, Wimmer, Zinner, & Tautz, 2002). Orangutan habitats are known for having low fruit production overall, and very unpredictable patterns of fruit availability, preventing these large-bodied adult apes from living in permanent association with others (Delgado & van Schaik, 2000; Galdikas, 1988; Harrison & Chivers, 2007; Knott & Kahlenberg, 2011; Mitani, 1989; van Schaik, 1999). Adolescent females establish an independent, but typically overlapping, home range from their mother (Knott et al., 2008). They will continue to visit their mothers often, especially in early adolescence, but also spend significant time alone and in association with others (van Noordwijk et al., 2009, 2012). Around the age of 15, female orangutans reproduce for the first time (Knott, 2001; van Noordwijk et al., 2018; Wich et al., 2009). They continue to associate periodically with their mother even after giving birth to their own offspring (Knott et al., 2008; van Noordwijk et al., 2012).

What differs for orangutans compared to other more gregarious female philopatric primates, however, is more dramatic physical separation from their mothers. Group-living female philopatric species remain within sight of their mother, and other related females, the vast majority of the time. Female–female close social bonds in such species have indirect and direct fitness consequences in the form of reduced stress (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Wittig et al., 2008), higher infant survival (Silk, Alberts, & Altmann, 2003), and higher reproductive success (Silk et al., 2009). In contrast, adolescent female orangutans spend most of their time far enough away from their mother that she is at least undetectable to human observers (Knott et al., 2008). Adolescent female orangutans have been identified as the most social age-sex class in Gunung Palung National Park (O'Connell, 2018; O'Connell & Knott, 2015) and elsewhere in Borneo (Galdikas, 1985; 1995; Carne, Semple, Morrogh-Bernard, Zuberbuhler, & Lehmann, 2013). They

independently initiate social associations with all other age-sex classes and with one another (O'Connell, 2018). Adolescent female orangutans, then, must develop relationships with conspecifics without the support of constant familial companions. Female orangutan home ranges overlap extensively and adolescents will inevitably encounter non-mother individuals (Knott et al., 2008), and must somehow navigate those encounters on their own.

Female orangutans do compete with one another for territory (Knott et al., 2008) and a rare but deadly case of an unflanged male–female dyad attacking another female has been documented (Marzec et al., 2016). Adolescent female chimpanzees experience aggression from resident females as they disperse from natal groups (Kahlenberg, Thompson, Muller, & Wrangham, 2008; Pusey, 1980; Pusey et al., 2008), and while adolescent female orangutans are not formally entering a new social group, they are similarly having to establish a new home range that may cause ranging conflict with other females. With a vulnerable baby to care for in an environment that has unpredictable resources and in a species with the capacity for social aggression, female orangutans must achieve ranging, foraging, and social competence before their first reproduction, making the adolescent period critical for survival and reproductive success.

Not only do adolescent female orangutans have to establish their own social connections with female conspecifics in the absence of regular kin support, they must also navigate sociosexual relationships with males. Orangutan males are known for their frequent sexually coercive tactics. Orangutan mating involves a high degree of resistance by females and forced copulation by males (Fox, 2002; Knott, 2009; Knott, Thompson, Stumpf, & McIntyre, 2010; Mitani, 1985; Utami Atmoko et al., 2009). With flanged males having double the body size of adult females (Markham & Groves, 1990) and mating often taking place upwards of 25 m high in the canopy (unpublished data from Gunung Palung), these hostile mating events pose potential risks to females. Despite these risks, adolescent female orangutans must begin mating if they are to achieve their first conception. Additionally, it has been argued that promiscuous mating is an effective anti-infanticide behavioral strategy employed by female orangutans (Knott et al., 2010; Knott et al., 2019), which would further necessitate adolescents establishing themselves in the sociosexual landscape if they are to effectively confuse paternity over their first offspring.

Male ambivalence toward nulliparous females is another challenge that female orangutans face during adolescence. Disinterest in mating with nulliparous females is observed widely across primates (Anderson, 1986; Muller, Thompson, & Wrangham, 2006; Scott, 1984; Smuts, 1985), and has been attributed to adolescent subfecundity and male preference for older, more experienced females (Muller et al., 2006; Scott, 1984). Adolescent female orangutans must overcome male ambivalence during limited social encounters while also protecting themselves from sexual coercion (Knott et al., 2019). As such, we expect them to display unique behavioral strategies compared to parous adult females.

There is some published evidence that adolescent females are more proactive in their sexual behavior than adult female

orangutans. Schürmann (1981, 1982) documented the behavior of a particular adolescent female–flanged male dyad at Ketambe Research Station, detailing the extremely proceptive behavior of the young nulliparous female that was directed toward the flanged male. He observed that an additional adolescent female began courting the flanged male in a similar fashion once the original consorting pair separated. Schürmann (1982) noted that consortships between parous females and adult males, both flanged and unflanged, were not nearly as proceptive on the part of the female. Utami Atmoko et al. (2009) mention nulliparous females being more proceptive than parous females, but no supporting details are provided.

To address the hypothesis that adolescent females have unique behavioral strategies compared to adult females, we test whether adolescent female mating behavior differs from that of adult females in the degree of proceptivity. We predict that adolescent females will display more proceptive behavior and less frequent resistant mating behavior compared to adult females. We also document the socio-sexual behavioral strategies of young nulliparous female orangutans during the precarious adolescent period by providing a detailed account of the sexual behavioral repertoire of adolescent females when in consort with flanged males during late adolescence and provide accounts of adult female mating behavior for comparison.

## 2 | METHODS

This study complied with protocols approved by Boston University's Institutional Animal Care and Use Committee and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates and the legal requirements of Indonesia.

### 2.1 | Study site

Gunung Palung National Park is a 108,000-hectare forest located in West Kalimantan, Indonesia on the island of Borneo. Within the park is the Cabang Panti Research Station (1130 S, 11070 E), an area of 2,100 hectares containing a trail system formed from transects. The study area contains seven different habitat types, including peat swamp, alluvial bench, freshwater swamp, lowland sandstone, lowland granite, upland granite, and montane forest (Marshall, Beaudrot, & Wittmer, 2014). Logging has taken place intermittently within and around the park since the 1960s (Johnson, Knott, Pamungkas, Pasaribu, & Marshall, 2005). Legal logging concessions were closed over 30 years ago (Johnson et al., 2005), but illegal hand-logging continues in parts of the park today. However, the interior of the park and Cabang Panti Research Station remain largely undisturbed (Marshall et al., 2009).

### 2.2 | Study period

Detailed behavioral data on social and mating interactions were collected from July 2013 to July 2014 by C. O'Connell. Detailed

mating data from 1994 to 2014, extracted from C. Knott's long-term database, were also used.

### 2.3 | Study subjects

The orangutans of Gunung Palung are members of the subspecies *Pongo pygmaeus wurmbii*. The broader study period (1994–2014) included mating data from 11 adolescent females (24 mating events), eight adult females (32 events), eight flanged males (29 events), and 17 unflanged males (27 events), in 56 total mating events. During the 2013–2014 study period, three adolescent females (Walimah, Dagul, and Betsy) and three flanged males (Codet, Prabu, and Moris) were observed engaging in long, elaborate mating events, detailed in this study.

Adolescent females are defined here as independently ranging and nulliparous, have not yet produced their first offspring. A female was considered an adult when she reproduced for the first time. Most adolescent females were either followed from birth or from when they were juvenile dependents. Age estimates for those that were first followed when they were juvenile dependents were based on achievement of independent ranging combined with the timing of the birth of a sibling and the average interbirth interval for orangutans (7.6 years; from van Noordwijk et al., 2018). A smaller subset of females was first encountered as adolescents and was only included if they were nulliparous and had the distinctive physical characteristics of adolescents such as lighter skin around their eyes, lighter hair, and other features of young females. Adolescents in this data set had known or estimated ages ranging from 13- to 15-year old. The average age at first reproduction is 15 years for orangutans (van Noordwijk et al., 2018). Females were classified as adults if they had a dependent infant or juvenile that ranged with them, slept in their nest, and nursed from them at least occasionally. For the aims of this study, the exact chronological age does not need to be known, as the developmental milestone of achieving first reproduction is the marker of interest for distinguishing adolescent versus adult females. To account for potential differences in mating tendencies for females of different reproductive states, we also recorded whether the female was potentially cycling or not. A female was considered potentially cycling if she was independently ranging, not pregnant, and had no dependent offspring younger than 8-years old. Sexually mature male orangutans come in two distinct forms (Knott & Kahlenberg, 2011; Utami Atmoko & van Hooft, 2004)—flanged and unflanged. Flanged males are larger in body size, have fatty cheek pads (or flanges) on the sides of their faces, produce long call vocalizations, and are dominant over unflanged males (Mackinnon, 1974; Mitani, 1985; Rijksen, 1978; Utami Atmoko & van Hooft, 2004). Unflanged males are independently ranging, having dispersed from their natal ranges. They lack the fatty cheek pads that flanged males display and are smaller in body size, though they are fully capable of siring offspring (Utami Atmoko et al., 2009).

## 2.4 | Behavioral data

Whenever sexual interactions took place, the identities of the actors and recipients, the time of initiation and termination of contact, and the type of behavior were recorded. A standard mating data sheet was used to document and code mating events in all cases, throughout both periods, using the same ethogram. Female mating behaviors were categorized into proceptive, receptive or resistant based on an ethogram (Table 1), following Knott et al. (2010). The number of occurrences of all such behaviors was tabulated for each mating. We then determined a mating score based on the combination of behavior types that were displayed during the event using the formula shown in Table 2. This produced a value that represented the degree to which the female was proceptive (10), resistant (1), or simply receptive (5).

## 2.5 | Data analysis

Descriptive statistics were calculated for mating score (mean, median, mode) and mating duration (mean, median), and mating behavior types (mean, range) for adolescent and adult females. Generalized linear mixed models with an ordinal distribution were used to predict the mating score. Only mating events of females who were potentially cycling (not pregnant or lactating) were included to limit our comparison to females who could potentially conceive and to avoid female mating driven by other possible motivations. For example, pregnant females have previously been shown to be proceptive towards males, possibly as a strategy for paternity confusion (Knott et al., 2010).

Female class (adolescent or adult), mating duration, and male type (flanged or unflanged) were used as fixed effects. Female and male IDs were used as random effects to account for multiple observations of the same individual. All statistical tests were performed in SPSS 25.

**TABLE 2** Mating score assigned to an event based on the combination of observed behaviors within a mating event

Score	Observed behaviors
1	All resistant
2	All resistant + 1–2 receptive behaviors
3	All receptive + 2–3 resistant behaviors
4	All receptive + 1 resistant behavior
5	All receptive, no proceptive, no resistant
6	All receptive + 1 proceptive
7	All receptive + 2–3 proceptive and/or 1 resistant
8	All proceptive + 1–2 receptive and/or 1–2 resistant
9	All proceptive + 1–2 non-proceptive
10	All proceptive

## 3 | RESULTS

### 3.1 | Adolescent versus adult female mating events

We compared mating scores (1–10) between adolescent and adult females in Gunung Palung National Park from 1994 to 2014 to test whether they differed in degree of proceptivity, with scores of 1 being fully resisted matings and scores of 10 representing fully proceptive matings. Adolescent females ( $N = 11$ ) had a mean mating score of  $7.4 \pm 2.5$  (median = 8, mode = 10, range = 2–10), whereas adult females ( $N = 8$ ) had a mean mating score of  $3.3 \pm 2.0$  (median = 2, mode = 2, range = 1–9). The mean adolescent female sexual contact duration was  $854 \pm 285$  s, whereas the mean adult female duration was  $486 \pm 65$  s.

Table 3 presents the mean number of acts and the mean rate of each behavior type in adolescent female and adult female mating events. Adolescent female events had mean rates of  $0.42 \pm 0.45$ ,  $0.43 \pm 0.43$ , and  $0.14 \pm 0.25$  of proceptive, receptive, and resistant behaviors, respectively. Adult female mating events had mean rates

**TABLE 1** List of mating behaviors separated into one of three categories—Receptive, proceptive, and resistant

Receptive behaviors	Proceptive behaviors	Resistant behaviors
Female and male side-by-side	Female approaches male	Female avoids male behavior
Female and male sitting face to face	Female helps with intromission	Female open-mouth threat
Female and male enter nest together	Female touches male genitalia with mouth	Female vocalizes against male approach
Female cooperative as mating begins	Female licks penis	Female runs away from male
Female stops struggling after mating begins	Female puts penis in mouth	Female tries to pull away from male
	Female spreads male legs	Female struggles against male
	Female sits on top of male	Female aggressive towards male before mating
	Female pulls on male leg in solicitation	Female aggressive toward male during mating
	Female pulls on male arm in solicitation	Female urinates
	Female performs pelvic thrusts	Female screams
	Female lays down on top of male	Female grumble
	Female displays genitalia to male	Female grumpf
	Female rubs genitalia on male	Female lork
	Female examines male genitalia visually	Female makes a small noise
	Female smells male genitalia	Female distress vocalization
	Female touches male genitalia with hand	
	Female positions herself under male	
	Female puts her genitalia against male genitalia	

**TABLE 3** Descriptive statistics for the different sexual behavior types in adolescent female versus adult female mating events

		Adolescent female	Adult female
Proceptive	Mean no. of acts per mating event	14.18 ± 33.10	0.37 ± 1.57
	Mean proportion per mating event	0.42 ± 0.45	0.05 ± 0.19
Receptive	Mean no. of acts per mating event	1.12 ± 0.99	1.04 ± 0.90
	Mean proportion per mating event	0.43 ± 0.43	0.43 ± 0.41
Resistant	Mean no. of acts per mating event	0.76 ± 1.15	1.93 ± 2.21
	Mean proportion per mating event	0.14 ± 0.25	0.52 ± 0.42

Note: Proportions of each behavior type are the percentage of the total acts performed per mating event under that category.

of  $0.05 \pm 0.19$ ,  $0.43 \pm 0.41$ , and  $0.52 \pm 0.42$  of proceptive, receptive, and resistant behaviors, respectively (Figure 1).

Using the generalized linear mixed models (GLMMs) to predict mating score, all combinations of possible two-way interaction effects were tested and subsequently omitted from the final model, as none of the interactions were significant. Female class significantly predicted mating score ( $p = .001$ ), whereas male type (flanged or unflanged) and mating duration did not significantly predict mating score ( $p = .309$  and  $p = .181$ , respectively; Table 4). Adolescent female mating events ( $N = 19$ ) had significantly higher mating scores (indicating more proceptivity) than did those of adult females ( $N = 26$ ;  $\beta = 1.948$ ,  $p = .001$ ; Table 5 and Figures 2 and 3).

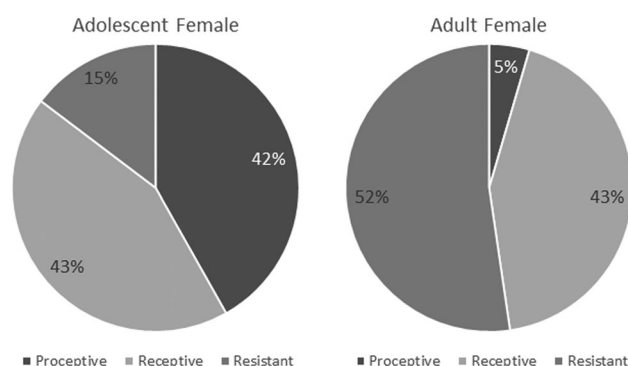
### 3.2 | Adolescent female–flanged male sociosexual interactions

The most extensively followed adolescent female during the study period was Walimah, an individual who has been followed in Gunung Palung National Park since her birth in 1998. Walimah has spent over 14,000 hr in the presence of humans as a focal individual, dependent offspring of a focal, or in social interactions associated with other focal animals (Knott et al., 2019). She is, thus, extremely well-habituated to observers. As one of the most extensively followed individual orangutans, we first detail her mating history to illustrate the changes in behavior over the adolescent period.

The first time Walimah was observed mating, was a forced copulation with an unflanged male when she was 10.4-years old. Despite many hours of observation, she would not be seen mating again

for 5 years. During the interim period, she spent 60% of her social time in the presence of adult males, both flanged and unflanged. Starting on August 1, 2013, when she was 15-years old, Walimah began an intensive period of following the flanged male, Codet, finally culminating in their first known mating after 6.5 months. During this period Walimah was encountered by observers on 53 different days. She spent a total of 4,199 min with Codet, with 480 of those minutes within 5 m of him, over 14 of those days. During these associations, she followed Codet closely and watched him intently from the same or a nearby tree. During these close associations, Codet would remain motionless while Walimah inspected him, including his penis, lightly touched him, and presented her genitals to him. If Codet moved suddenly, Walimah would avoid him, running away and hesitating before resuming following him. During these close examinations, no mating or mating attempts occurred. During this period Walimah also occasionally traveled with other males, including two different unflanged males, a partially flanged male (small cheek pads emerging, had the ability to long call), and a different fully flanged male. However, these associations only rarely included instances of mildly proceptive behavior by Walimah in the form of genital inspection. There were several instances of affiliative physical contact with unflanged males, but no mating or mating attempts.

After months of Walimah's frequent interactions with males, where no mating was observed, Walimah copulated with Codet on March 20, 2014, when she was 15.4-years old. The event was initiated by Walimah and began with prolonged manual (4 bouts) and oral stimulation (10 bouts) of Codet's penis, along with multiple attempts at intromission (3 bouts of female pelvic thrusts) on her part. Walimah moved Codet's legs to better access his genitals three different times. Throughout the event, Codet remained still, with his arms extended above his head, holding onto branches for support. His head was tilted back, with his gaze averted from Walimah. After 26 min of these highly proceptive

**FIGURE 1** Mean proportion (as a percentage of all acts performed) of each behavior type in adolescent female versus adult female mating events**TABLE 4** Results of generalized linear mixed model-predicting mating score based on female age-class, status of male mating partner (flanged or unflanged), and mating duration

	F	df1	df2	p Value
Corrected model	5.451	3	41	.003
Female age-class (adolescent or adult)	11.646	1	41	.001
Male class (flanged or unflanged)	1.063	1	41	.309
Mating duration	1.851	1	41	.181

Significant effects are in bold.



**TABLE 5** Fixed coefficients from generalized linear mixed model-predicting mating score based on female age-class, status of male mating partner (flanged or unflanged), and mating duration

Model term	Coefficient	Standard error	T	p Value	95% CI lower	95% CI upper
Adolescent female	1.948	0.571	3.413	<b>.001</b>	0.745	3.10
Adult female	0 <sup>a</sup>					
Unflanged male	-0.521	0.505	-1.031	.309	-1.540	0.499
Flanged male	0 <sup>a</sup>					
Mating duration	0.001	0.001	1.360	.181	-0.000	0.002

Abbreviation: CI, confidence interval.

Significant effects are in bold.

<sup>a</sup>This coefficient is set to zero as it is redundant.

behaviors by Walimah, with Codet remaining in the afore-described pose, Codet became active, achieving intromission and performing pelvic thrusts for 2 min until he (presumably) ejaculated and the mating event ended after 28 total minutes of physical contact. The dyad remained in consortship for several more days, with two additional and nearly identical mating events taking place on March 21st—one event lasting 15 min and one lasting 23 min.

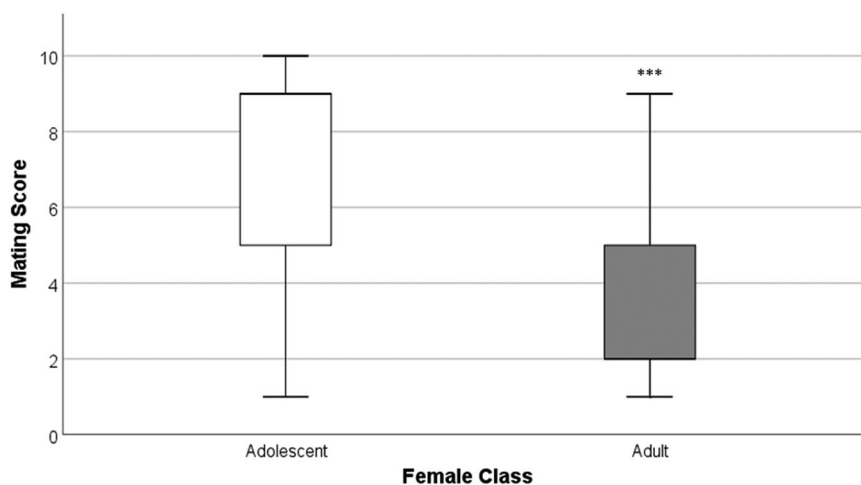
A strikingly similar mating interaction was observed between another dyad on March 26, 2014, within days of the Walimah–Codet events, between adolescent female Betsy and flanged male Moris. Their sexual contact lasted for 114 min and was initiated by Betsy. This event contained an even greater diversity of proceptive behaviors over its nearly 2-hr course, including Betsy thrusting her genitals on Moris's face and mouth (4 bouts) and using Moris's hand or foot to masturbate herself (2 bouts), in addition to the repeated interspersed bouts of oral stimulation, manual stimulation, and attempted/achieved intromission and thrusting by Betsy. Moris did perform pelvic thrusts intermittently throughout the event, but his bouts were brief, shallow, and subtle. For the most part, he remained still, arms typically raised and grasping branches, while averting his gaze from Betsy, though she performed a range of proceptive sexual behaviors.

The commonalities in all events between Walimah–Codet and Betsy–Moris include the extensive proceptive behavior by the adolescent female (touching the male, attempting intromission, placing genitals to the face and penis of the flanged male, performing

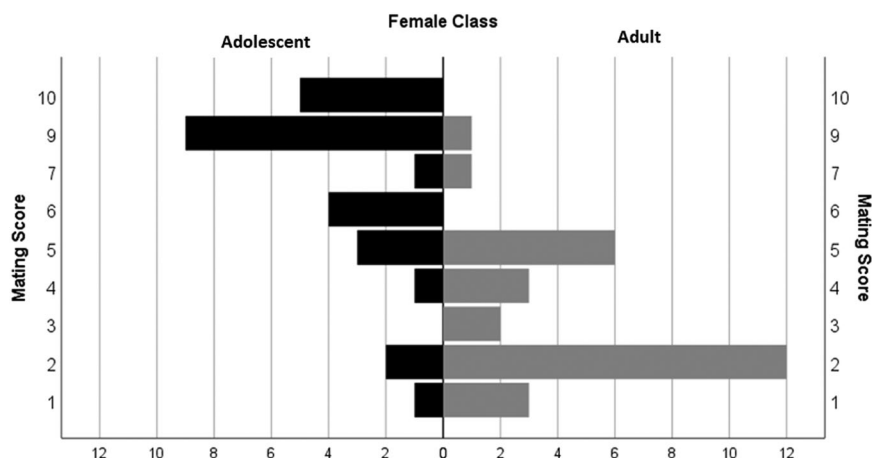
oral stimulation of the male's penis), the stillness and posture of the flanged male (see Figure 4), and the long duration of the sexual contact. Additionally, in each of these cases, the adolescent female was an older adolescent, having been ranging independently for several years. Walimah was 15-years old when these elaborate mating interactions were first witnessed in March of 2014 and she conceived for the first time in July 2014. Betsy was 14-years old ( $\pm 6$  months) at the time of her mating event with flanged male Moris and had been ranging independently since February 2011. As of November 1, 2016, Betsy was not known to be pregnant, but she has not been seen again since that date. A third dyad, Dagul–Prabu, also displayed extensive physical contact (embracing) and oral stimulation of the male Prabu by adolescent female Dagul over the course of 15 min of sexual contact on May 25, 2014, though this never resulted in mating. Dagul was 14-years old at the time.

### 3.3 | Adult female–flanged male sexual interactions

For comparison, we describe typical adult female–flanged male sexual interactions near the time of conception at Gunung Palung. On December 16, 1997, parous adult female Marissa was in consortship with flanged male Jari Manis. Jari Manis approached Marissa to initiate physical contact and proceeded to mate with her for a total of 5 min. Marissa was receptive to Jari Manis but did not display any

**FIGURE 2** Box plot of mating scores for cycling adolescent females versus cycling adult females showing a significant difference, with adolescent females having higher (more proceptive) mating scores than adult females ( $p = .001$ )

**FIGURE 3** Histogram of the mating scores for cycling adolescent and cycling adult females. Each bar represents the number of mating events receiving that mating score. The scores 1–10 represent the most proceptive of mating (10), the most resisted mating (1) and neutral, unresisted mating (5)



proceptive behavior. We know that Marissa was ovulating at this time from hormonal data (Knott et al., 2010). On March 25, 2014, adult female Bibi was 3 months from conceiving her second offspring and had been observed mating regularly for about 9 months prior. In consortship with flanged male Codet, Codet approached Bibi and initiated contact, and performed pelvic thrusts for 6 min. Bibi displayed no resistant behavior but also, no proceptive behavior. These two accounts are representative of adult female mating

events, though many others also contain resistant behaviors. One particularly proceptive event involving an adult female was documented on January 16, 1998. Parous female Zarina approached flanged male Jari Manis and initiated physical contact. She pulled on his arm and leg in solicitation and assisted with intromission using her hand once. She performed some of the pelvic thrusts and the mating lasted for 16 min. We know from hormonal data that Zarina was ovulating at the time (Knott et al., 2010). Though clearly proceptive, this event was not as intense as the previously described adolescent female events as it did not involve any of the manual and oral stimulation of the male's penis that the adolescent female events were characterized by and there was no indication of the male sitting completely still with his gaze oriented away from the female. This was the most proceptive mating event involving an adult female in our database.



**FIGURE 4** A still shot from a video (filmed by Robert Rodriguez Suro) of flanged male, Codet, during a sexual interaction and mating event with adolescent female, Walimah. Of note are his raised arms and his head tilted back as he looks upwards. This position is typical of the events witnessed at Gunung Palung and also for those described by Schürmann (1981, 1982) at Ketambe on Sumatra

## 4 | DISCUSSION

Adolescent female mating events were characterized by a higher degree of proceptivity compared to those of adult females. Male type (flanged or unflanged) was not a significant predictor of the degree of proceptivity displayed by a female. It was previously believed that forcing copulations was a strategy specific to unflanged males (Galdikas, 1981; Rijksen, 1978; Schürmann & Hooff, 1986), but females do resist mating with both types of male (Fox, 2002; Knott et al., 2010; Mitani, 1985; Utami Atmoko et al., 2009). Though flanged males have been shown to be preferred mates for female orangutans, particularly at times when they can potentially conceive (Knott et al., 2010), adolescent females have proceptive matings with both unflanged and flanged males. The proceptive events with unflanged males, however, were not as involved and elaborate as the events we have detailed here involving flanged males, and no events involving unflanged males from the long-term database have noted stillness or a receptive posture of an unflanged male.

Although adult females often cooperate and are receptive during mating events, they rarely, if ever, engage in such intensive proceptive behavior as is observed with adolescent females. Over

the same 2013–2014 study period that contained the adolescent events we detail here, adult females were also observed mating 11 different times, seven of which involved a cycling adult, but none of those events resembled those between Walimah and Codet or Betsy and Moris. This difference in the degree of proceptive behavior supports the idea that different mating strategies are necessary for females at different stages in the life course.

The sexual interactions between adolescent females and flanged males were characterized by three main commonalities: (a) extreme proceptive behavior, (b) exceptionally long duration, and (c) the stillness and posture of the flanged male. Taken together, these event characteristics indicate a high degree of investment in the interaction on the part of both the adolescent female and the flanged male.

The adolescent females performed a wide variety of sexual behaviors over the course of many minutes, and in one case, hours. Many of the acts did not involve intromission. One possibility for explaining why females would spend time and energy on these behaviors is that females need experience to effectively copulate, as female orangutans are often responsible for positioning themselves during intromission, at least during proceptive matings. It often appeared during these adolescent events that intromission was not achieved despite the female's efforts to do so.

While inexperience may explain some parts of adolescent mating behavior, we suggest that the elaborate efforts by the female are to overcome male ambivalence towards them. Nulliparous female primates are typically not preferred mating partners and males display a low degree of interest in copulating with them (Anderson, 1986; Baniel, Cowlishaw, & Huchard, 2016; Galdikas, 1981; Muller et al., 2006; Parga, 2006; Setchell & Wickings, 2006). Accordingly, young adolescent female orangutans that pursue flanged males are often ignored and their presence merely tolerated. For example, Walimah's early associations with Codet involved Walimah approaching Codet and placing her face or her genitals close to his face while he simply continued feeding without giving her a second look. They were only observed mating starting in March 2014, long after Walimah was first recorded following him for extended periods starting in August 2010 and then in 2011. It is possible that this long period of disinterest on the part of males is due to adolescent subfecundity—the period after menarche but before conception during which adolescent females are cycling, but hormone production may be insufficient for a successful pregnancy (Young & Yerkes, 1943; Gilbert & Gillman, 1960; Bercovitch & Ziegler, 2002; Knott, 2001). It is only later in adolescence, when orangutan females have been ranging independently for several years that these elaborate mating events seem to begin. The few data points we have from Gunung Palung of young adolescent females mating are exclusively with unflanged males and the events are either totally resisted by the young females or are moderately receptive. No proceptive matings have been recorded in females under 13 years of age.

The average mating duration for an adult female was 8 min, whereas the average mating duration for an adolescent female was 14 min, though these can last up to 2 hr as we have described here. It is not clear what might cue a flanged male to turn from indifference

to willful participation in these prolonged events with adolescents that require, at the very least, a time investment. Perhaps the adolescent female has gained confidence after many associations with the male and her extreme proceptive behavior signals that she is ready for mating. Orangutans lack the sexual swellings that some catarrhine primates display to signal their reproductive status, but it is possible that other cues are in place to stimulate the interest of the male once a female is ready to conceive. It has been suggested that adolescent subfecundity may function to allow “neophyte females” time to discern appropriate sires without the risk of conception with a potentially undesirable mate (Bercovitch & Ziegler, 2002). Towards the end of the adolescent period when female orangutans are better prepared to conceive, they may need to put in extra effort to convince a male of their readiness and suitability as a mating partner.

Copulation rates in orangutans are low relative to chimpanzees (Stumpf, Thompson, & Knott, 2008) and bonobos (Furuichi & Hashimoto, 2002; Hashimoto & Furuichi, 2006). Traveling in consortship with a female is costly in terms of longer daily path lengths for flanged males (Utami Atmoko, 2000; Utami Atmoko & van Hoof, 2004). Flanged males have also been shown to consume less energy per unit body mass than other age-sex classes, which they compensate for through shorter active periods and shorter day journeys (Vogel et al., 2017). Engaging in consortship with a female that is unable to conceive may be pushing flanged males to the brink of energetic viability without the potential payout of reproductive opportunity. For this reason, flanged males may need to be convinced of a young female's reproductive potential before they are willing to invest their limited energy in them.

The flanged males involved in these events held a posture and remained remarkably still for these extended periods. Flanged males are at least double the size of an adolescent female (Leigh & Shea, 1995; Utami Atmoko & van Hoof, 2004) and, like unflanged males, can force females to copulate (Knott et al., 2010; Utami Atmoko et al., 2009), which would accomplish a mating in a shorter time (Knott, 2009). If they were uninterested in the female they could be spending this time doing any number of other activities that might be beneficial to them, such as eating, resting, or mating with a different female. Instead, they remain motionless with their arms raised and allow the female to carry out many sexual behaviors. This is a clear departure from the ambivalence shown towards younger adolescent females. There must be new benefits that males reap by changing their approach with adolescent females as they age. Although the females are able to signal their conceptive readiness to flanged males with these intensive behaviors, males are also able to signal their willingness and agreeable temperament to the female.

In our data, we witnessed repeated matings between specific adolescent female–flanged male pairs. We, thus, suggest that the most likely explanation for male tolerance of these adolescent female interactions, and their nonaggressive participation in these long mating events, is that it may increase the chances that she seeks him out specifically, when she is fully mature. Considering that orangutan interbirth intervals are 7.6 years long, on average, (van Noordwijk et al., 2018), these flanged male behaviors may help him ensure that



he is the sire of her first offspring. Adolescent females are characteristically nervous around flanged males, avoiding their sudden movements and showing behavioral signs of anxiety in their presence (O'Connell, 2018; O'Connell, Thompson, & Knott, 2017). The signature stillness and receptive body position of the flanged male may be a way for him to signal to the female that he is nonthreatening, gaining her trust to initiate the physical contact necessary for mating. A similar argument has been made by van Noordwijk and van Schaik (2009) regarding food theft from males by females. They suggest that it is a way for female orangutans to test a male's temperament and tolerance toward her. Without permanent group associations, male orangutans risk a periovulatory female terminating an association with them, thereby losing a siring opportunity. Flanged males have been shown to adopt a "sit and wait" mating strategy, emitting long-distance calls to attract females to their location (Delgado, 2007; Mackinnon, 1974; Mitra Setia & van Schaik, 2007; Rijksen, 1978; Utami Atmoko & Mitra Setia, 1995). By tolerating both time-intensive sexual behaviors and the theft of food by adolescent females, flanged males ensure that young females develop familiarity with them and will choose to approach them when conception is likely.

We suggest that these adolescent female–flanged male sociosexual events are a genus-wide phenomenon and an integral part of female orangutan sociosexual development during late adolescence. In addition to the events documented here, Schürmann's (1981, 1982) accounts from Sumatra in *Pongo abelii* are remarkably similar. Nulliparous female, Yet, showed great interest in flanged male Jon and followed him around, inspecting him, touching him, and taking food from him. After months of Yet following Jon, they finally mated. The events involved oral and manual stimulation of the male's penis by the female and the female's attempted intromission. The flanged male, Jon, was motionless during copulation and looked away from the female. Schürmann (1981, p. 131) termed the posture of the male as "male presenting," in which Jon assumed "...upright sitting position, usually extended his arms and legs and bent backwards until he almost lay on his back. This particular pattern of presenting was only observed in the adult male Jon; it was never seen in subadult males." These elaborate matings occurred shortly before Yet conceived for the first time.

A survey of colleagues from other orangutan study sites also confirms the occurrence of similar events at additional locations across the range of orangutans (see the Supporting Information Material). These accounts support the suggestion that these intensive mating events are exclusive to adolescent female and flanged male dyads, specifically, and that they are consistent in involving extensive female proceptive behavior, long duration, and a specific male body position in populations throughout the range of the genus *Pongo*. We suggest that "male presenting" be incorporated into existing ethograms of long-term studies of orangutans.

If the accounts described here are characteristic of older adolescent females and flanged males across the genus, why are these events observed infrequently despite many years of continuous monitoring of several orangutan populations? First,

the aims of long-term research studies and the demographic make-up of the study population at any given time may preclude adolescent females from being followed with regularity. Given the semisolitary nature of orangutans, if observers are not encountering adolescent females or targeting them as focal animals, the chances of witnessing these apparently rare events are greatly reduced. Some study sites have low population densities which make following an appropriately-aged adolescent female particularly difficult (A. Russon, May 25, 2019 personal communication). Second, it may be that the energetic status of the adolescent females needs to be sufficiently positive for these interactions to take place. The period over which the extremely proceptive adolescent female–flanged male sexual interactions took place was brief, spanning just 2 months. It is possible that ecological conditions need to be adequate for individuals to be able to afford the time and energy investment that these interactions require. While the months of March, April, and May 2014, when the events took place, were not exceptionally high-fruited periods at Gunung Palung, they were preceded by peaks in fruit availability and energy intake in December 2013 and February 2014 (O'Connell, 2018; O'Connell & Knott, 2015). The combination of having several similarly aged older adolescent females in the study area and adequate energetic reserves may have created the ideal conditions for researchers to observe this behavior. As seemingly anecdotal data on rare events build, we can gain insight into behaviors that may be significant to this long-lived and cryptic species.

We suggest that this particular behavioral repertoire may be unique to orangutans because of the unusual pattern of forced copulation in this genus coupled with their dispersed social organization. Adolescent female orangutans must establish a rapport with flanged males independent of their mother or other kin, unlike more gregarious species. Sumatran orangutan researchers have suggested that females distribute themselves within the home range of a dominant flanged male and receive protection from sexual harassment from other males as a result (Fox, 2002). It is also expected that infanticide is a risk for orangutan mothers (Knott et al., 2019; Knott et al., 2010; Scott, Knott, & Susanto, 2019; but see Beaudrot, Kahlenberg, & Marshall, 2009). Establishing familiarity with a resident flanged male could allow adolescent females to seek proximity with him, when necessary, to reduce her future risk of harassment by sexually coercive males.

The function of these elaborate events may be elucidated by identifying the sires of first offspring. Utami Atmoko, Goossens, Bruford, de Ruiter, & van Hooff (2002) found that unflanged males sired roughly half of the offspring at Ketambe Research Station on Sumatra, but presented tentative evidence that unflanged males are more likely to sire firstborn offspring than are flanged males (Utami Atmoko et al., 2009). Half of the firstborn infants sired by unflanged males were born to ex-rehabilitant mothers. Wich et al. (2004) found that Ketambe females born to ex-rehabilitant mothers had accelerated development and earlier ages of first birth compared to wild females or those born from wild mothers,

which they speculate is due to the better energetic conditions of their mothers. Thus, many of the nulliparous females in the Utami Atmoko et al. (2002) study may have been fecund at an earlier age than is typical for wild females. As young nulliparous females have a period of voluntary consortship with unflanged males earlier in adolescence when flanged males are uninterested, the ex-rehabilitant status could have influenced the likelihood of unflanged male sires in the population (Utami Atmoko et al., 2009). Nonetheless, it will be useful to test whether the less desirable male morph (Knott et al., 2010; Utami Atmoko et al., 2002) has higher reproductive success with nulliparous females than experienced mothers at other research sites. Genetic studies will be able to determine the paternity of infants born to primiparous females and thus will be able to test the hypothesis that these long sexual events serve to increase the chances that a flanged male will sire a female's first offspring. Examining how the social dynamics between these adolescent females and their flanged male partners persist or change over time will also contribute to our understanding of the function of flanged male investment in these prolonged mating interactions and clarify the benefits to adolescent females during this important transitional phase in their life history.

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## CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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## SUPPORTING INFORMATION

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

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