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RESEARCH ARTICLE

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Alternative reproductive tactics of unflanged and flanged male orangutans revisited

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Abstract

In many slowly developing mammal species, males reach sexual maturity well before they develop secondary sexual characteristics. Sexually mature male orangutans have exceptionally long periods of developmental arrest. The two male morphs have been associated with behavioral alternative reproductive tactics, but this interpretation is based on cross-sectional analyses predominantly of Northwest Sumatran populations. Here we present the first longitudinal analyses of behavioral changes of 10 adult males that have been observed in both unflanged and flanged morph. We also analyzed long-term behavioral data on an additional 143 individually identified males from two study sites, Suaq (Sumatra, *Pongo abelii*) and Tuanan (Borneo, *Pongo pygmaeus wurmbii*), to assess male mating tactics cross-sectionally in relation to population, male morph (unflanged and flanged), and other socio-ecological factors. Both our longitudinal and cross-sectional results confirm and refine previous cross-sectional accounts of the differences in mating tactics between the unflanged and the flanged male morphs. In the unflanged morph, males exhibit higher sociability, particularly with females, and higher rates of both copulation and sexual coercion than in the flanged morph. Based on our results and those of previous studies showing that females prefer flanged males, and that flanged males have higher

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Abbreviations: ARTs, alternative reproductive tactics; CI, confidence interval; SD, standard deviation; SSCs, secondary sexual characteristics.

reproductive success, we conclude that unflanged males face a trade-off between avoiding male-male contest competition and gaining mating access to females, and thus follow a "best-of-a-bad-job" mating strategy.

KEYWORDS

developmental arrest, forced copulation, male bimaturism, reproductive strategies, sexual coercion

1 | INTRODUCTION

Males may employ alternative reproductive tactics (ARTs) to maximize their fitness (Gross, 1996; Oliveira et al., 2008). Individual tactics may either be fixed over the lifetime or plastic, whereby switches may occur either flexibly or sequentially, either in irreversible or reversible sequence (Taborsky et al., 2008). While the evolution of ARTs, and especially their ecological determinants, are still not completely understood (Engqvist & Taborsky, 2016), they have been documented in all major animal taxa (Oliveira et al., 2008). Male ARTs are less common in mammals, and frequently involve behavioral rather than morphological differentiation (Wolff, 2008).

The delayed development of secondary sexual characteristics (SSCs) relative to sexual maturity in mammals may reflect the context of sequential, alternative reproductive strategies (Setchell & Lee, 2004; Wolff, 2008). Females usually prefer males with SSCs compared to males who do not (yet) exhibit SSCs (review: Andersson, 1994; *Pongo abelii*: Fox, 1998; *Chlorocebus aethiops*: Gerald et al., 2010; *Propithecus verreauxi verreauxi*: Lewis & van Schaik, 2007; *Mandrillus sphinx*: Setchell, 2005; *Macaca mulatta*: Waitt et al., 2003), resulting in higher reproductive success for males with SSCs. However, before the development of SSCs, males may already gain some reproductive success, as they may avoid the costs of direct contest competition and are sometimes even tolerated by the males with SSCs providing a niche for ARTs (Gross, 1996; Oliveira et al., 2008).

Male orangutans (*Pongo* spp.) exhibit an exceptionally long phase before developing SSCs—unique in the primate order and mammals in general. The two distinct orangutan male morphs are referred to as unflanged and flanged. Flanged males exhibit fully developed SSCs including flanges (cheek pads), increased body size (~80 kg, up to twice the size of female orangutans: Markham & Groves, 1990), and an enlarged laryngeal sac, which enables them to emit long calls (Galdikas, 1985a; Kuze et al., 2005; Mitani, 1985b). Unflanged males lack SSCs, but have fully developed testicles (Dahl et al., 1993), reproduce successfully in the wild (Goossens et al., 2006; Utami, 2002), and continue to grow in body size (Leigh & Shea, 1995). The duration of the unflanged stage appears to be highly variable (Dunkel et al., 2013), but detailed data from wild populations are still largely missing, because of orangutans' slow life history (one study documents a wild individual remaining unflanged for 20 years before developing SSCs: Utami Atmoko & van Hooff, 2004). The final transition from the unflanged to the flanged male morph occurs within a few months and is accompanied by a peak in testosterone levels (captivity: Maggioncalda et al., 1999; wild: Marty et al., 2015; rehabilitation centers: Prasetyo, 2019). Flanging is irreversible and its immediate triggering mechanism remains unknown, but has been linked to social factors (Emery Thompson et al., 2012), most prominently unstable dominance relationships among flanged males (Utami Atmoko & van Hooff, 2004).

Our knowledge of reproductive success of the two morphs is limited, as siring opportunities are not only rare because of long female inter-birth intervals of 6–9 years (van Noordwijk et al., 2018), but also scattered in space because of orangutans' semi-solitary lifestyle (van Schaik, 1999). Moreover, female orangutans do not advertise the probability of ovulation with any behavioral or morphological signals (Durgavich et al., 2023; Galdikas, 1981; Schultz, 1938) and ovulation is likely concealed from males, as males initiate copulations even when females are highly unlikely to be fertile (Knott et al., 2010; Kunz et al., 2022; Nadler, 1981).

The unflanged and flanged morphs appear to exhibit ARTs. Flanged males are dominant over unflanged males and also highly intolerant of each other (Dunkel et al., 2013; Mitani, 1985b; Spillmann, Willems, et al., 2017; Utami Atmoko, Singleton, et al., 2009). Genetic evidence suggests that flanged males achieve most paternities (Banes et al., 2015; Tajima et al., 2018; van Noordwijk et al., in review), whereas unflanged males at least sire some offspring (Goossens et al., 2006; Utami, 2002). Flanged males are preferred by females: receptive, adult females actively approach long calls of dominant, flanged males (Mitra Setia & van Schaik, 2007) and initiate mating with them (Fox, 1998; Knott et al., 2010; O'Connell et al., 2019; Schürmann & van Hooff, 1986). Accordingly, it has been suggested that flanged males follow a "call-and-wait" mating strategy (Utami Atmoko & van Hooff, 2004), associating and copulating selectively with fertile females.

Evidently, given the female preference for and the greater competitive strength of flanged males, it would be advantageous to pass through the unflanged stage as quickly as possible, and to make the "best-of-a-bad-job" (Dawkins, 1980) while males wait to flange. Unflanged males are more tolerant towards each other, especially in some Sumatran populations (Galdikas, 1985b; Sugardjito et al., 1987), and are often tolerated by flanged males at some distance (Mitani, 1985a; Schürmann & van Hooff, 1986). Unflanged males do not emit long calls, rather, they roam widely and frequently approach and associate with females ("go-and-search" tactic: Utami Atmoko & van Hooff, 2004), and are more likely to force copulations in most study populations (Galdikas, 1985b; Utami Atmoko, Mitra Setia, et al., 2009; Utami Atmoko & van Hooff, 2004), a form of sexual coercion (Smuts & Smuts, 1993).

A model-based approach combining male orangutan life history traits and socio-ecology suggests that a period of developmental arrest in the unflanged morph is expected where there is (i) a highly male-biased operational sex ratio and thus intense male-male contest competition over access to fertile females, (ii) high monopolization potential by dominant males, i.e., those who outcompete other males in direct contests, (iii) low unflanged male mortality, and (iv) a nonzero rate of reproductive success for unflanged males (Pradhan et al., 2012). Thus, males would do better remaining unflanged as long as their chances of becoming dominant are minimal. A shorter delay would be selected for if the monopolization potential of a locally dominant (flanged) male falls below a threshold value (e.g., *sensu* Taborsky & Brockmann, 2010), which would allow other flanged males to gain enough paternities to make the switch worthwhile. In line with these theoretical predictions, the higher unflanged to flanged male ratio is indicative of a prolonged period of developmental arrest in Northwest Sumatran populations (*Pongo abelii*) (Delgado & van Schaik, 2000; Dunkel et al., 2013), where the monopolization potential is higher because of more abundant and less seasonal food sources compared to Bornean (*Pongo pygmaeus*) populations (Kunz, Duvot, van Noordwijk, et al., 2021; Mitra Setia et al., 2009; Roth et al., 2020).

Our current insight on orangutan alternative reproductive strategies is limited, as individual-based longitudinal analyses are lacking. All the patterns discussed above are based on cross-sectional data, predominantly from Sumatran populations. The considerable variation in these patterns reported between populations and species (Knott, 2009; Utami Atmoko, Mitra Setia, et al., 2009; Table 1) may be artefacts of modest sample sizes and short study durations (e.g., less than 3 years for most Bornean populations in Utami Atmoko, Mitra Setia, et al., 2009). Therefore, the effect of confounding variables, including ecological factors, the presence of fertile females, male dominance relationship stability and individual variation remains unknown.

The aim of this study is to provide the first longitudinal analysis assessing behavioral changes in association patterns, copulation frequency and the proportion of forced copulations over the transition from unflanged to flanged stage for six individual male Bornean (*P. pymaeus wurmbii*, at Tuanan) and four Sumatran (*P. abelii*, at Suaq) orangutans. Based on earlier cross-sectional studies, we predicted that while males are unflanged, they would (i) have higher association rates with females, (ii) maintain longer associations, (iii) remain in closer proximity to females, (iv) exhibit higher copulation rates, and (v) coerce mating more frequently, than after flanging. In addition, we conducted an extensive cross-sectional analysis at the individual level and across study site to evaluate possible socio-ecological effects on the association patterns with females, copulation frequency and the proportion of forced copulations by the two male morphs (van Schaik, 1999; Wich et al., 2011). All predictions are compiled in Table 1.

2 | METHODS

2.1 | Study sites and subjects

We analyzed long-term behavioral data from two study sites: Suaq (Sumatra), Gunung Leuser National Park, South Aceh, Indonesia (03°02'N; 97°25'E), and Tuanan (Borneo), Mawas Reserve, Central Kalimantan, Indonesia (02°15'S; 114°44'E). Both study areas are situated in peat-swamp forests with high orangutan densities of 7.44 (Suaq) and 4.5 (Tuanan) individuals per km^2 (Husson et al., 2009). At Suaq, over 3953 focal follow hours of adult males and 8504 focal follow hours of adult and adolescent females were collected between June 2007 and March 2018. At Tuanan, a total of 25,325 focal follow hours of adult males and 41,713 focal follow hours of adult and adolescent females were collected between June 2003 and July 2018.

We determined the unique individual identity of each focal subject by visual inspection of photographs as well as genotype data from non-invasively collected fecal samples (Arora et al., 2010, 2012; van Noordwijk et al., in review). Because orangutan males roam widely (Singleton et al., 2009) and are often absent from the study area for several months up to years (Figure 1 and Figure S2), their identification can be challenging. Therefore, we considered only males that were identified with certainty by several independent observers directly or from photographs, if genotype data were not available for a given sighting, resulting in data on 154 individually recognized males (Suaq: $N = 70$; Tuanan: $N = 84$; Table 2). Males were labeled as *flanged*, when they exhibited fully developed cheek pads, an enlarged throat sac and emitted long calls (Figure 1; Marty et al., 2015). *Unflanged* males included all sexually mature males without SSCs, after their natal dispersal, i.e., males with low relatedness to local adult females, and thus excluded young males before dispersal, i.e., with a known mother in or around the study area.

During the study period, 4 males at Suaq and 6 males at Tuanan were observed in both the unflanged and flanged morph states (Figure 1b,c). They flanged in different years (Figure 1). The transition from the unflanged to the flanged morph occurred within less than a year, and males were relatively rarely observed during this flanging period (Figure 1). While the exact timing of the onset of flanging was unclear, with large unflanged males sometimes exhibiting very small protrusions on their cheeks for several years, the boundary between flanging and flanged was very clear, with males suddenly having fully expressed SSCs as described above. To ensure that ambiguity in the onset of flanging did not obfuscate our longitudinal analysis and to account for variability within morph stage, we analyzed the data by *years to/since flanged*, whereby time 0 indicates when a male was observed with fully grown flanges for the first time.

Female orangutans are philopatric (Arora et al., 2012) and therefore, regularly observed in the study area, and more readily identified by researchers compared to males. In this study, we include both nulliparous females, who have been observed to copulate but had not yet given birth to their first offspring, and parous females. Because female orangutans do not exhibit any apparent signal of fertility or ovulation, it remains difficult to assess a female's

TABLE 1 Summary of hypothesized and observed differences in (behavioral) characteristics of unflanged and flanged male orangutans and variation between study populations.

	Male morph			Empirical evidence		Population/species variation		
Variable	**Unflanged**		**Flanged**	**Cross-sectional**	**Longi-tudinal**	**Sumatra[a] (*P. abelii*)**		**Borneo (*P. pygmaeus*)**
Developmental arrest of secondary sexual characteristics	Up to 20 years			Delgado & van Schaik (2000); Dunkel et al. (2013)	*anecdotal* (Utami, 2002)	Longer	>	Shorter
Habitat productivity				Wich et al. (2011)		Higher	>	Lower
Association frequency with…	Higher	>	Lower	Mitra Setia et al. (2009); Roth et al. (2020); van Schaik (1999)	*This study*	NW Sumatra	>	Borneo
Females (independent of fertility status)	Higher	>	Lower	Fox (1998); Galdikas (1985b), 1985a; Mitani (1985a); Schürmann & van Hooff (1986); Utami Atmoko, Mitra Setia, et al. (2009); Utami Atmoko, Singleton, et al. (2009)	*This study*	Higher	>	Lower
Fertile females (consortships)	ufm tolerated around consortships	<	flm monopolize		*This study*	Dominant flm monopolize access		
Unflanged males	Low	~	Low		Table S1	Higher	>	Lower
Flanged males	Low	>	Very low		Table S1	Very low	=	Very low
Proximity to females	Frequent	>	Selective: fertile or other males present	*This study*	*This study*	Lower	<	Higher
Copulation frequency	Less selective	>	Selective	Knott & Kahlenberg (2007); Utami Atmoko, Mitra Setia, et al. (2009)	*This study*	Consequence of higher association frequency	>	Consequence of lower association frequency
Forced copulations	Frequent	>	Rare	*This study*	*tbt*		>	
Dominance relationships	Subordinate	<	Dominant	Utami Atmoko, Singleton, et al. (2009)	*tbt*	More stable among flm	>	Less stable among flm
Evidence for physical fights	None	<	Frequent	Dunkel et al. (2013); Utami Atmoko, Singleton, et al. (2009)	*tbt*	Less?	<	Injuries + direct observations
Reproductive success	Low	<	High	Banes et al. (2015); Goossens et al. (2006); Utami (2002)	*tbt*	High skew towards one dominant flm?		Skewed towards several flms?
Emission of long calls	No		Yes	Askew & Morrogh-Bernard (2016); Mitani (1985b); Setia & van Schaik (2007); Spillmann, Willems, et al. (2010, 2017)	*tbt*	Dominant flm with high long-call rate		Confrontational assessment flm
Function of long calls					*tbt*	Mate attraction; females in earshot		M-M competition mate attraction

Note: The content of this table exceeds the scope of the current study but illustrates the main hypotheses/observed patterns. In the current study Suaq represents the Sumatran, Tuanan the Bornean study population.

[a] *Pongo tapanuliensis* is not included in this overview (Nowak et al., 2017), as limited empirical data on male reproductive strategies are available to this date; for association frequencies in Eastern Sumatran and *P. tapanuliensis* populations see Roth et al., 2020.

flm = “flanged male.”

ufm = “unflanged male.”

tbt = “to be tested.”

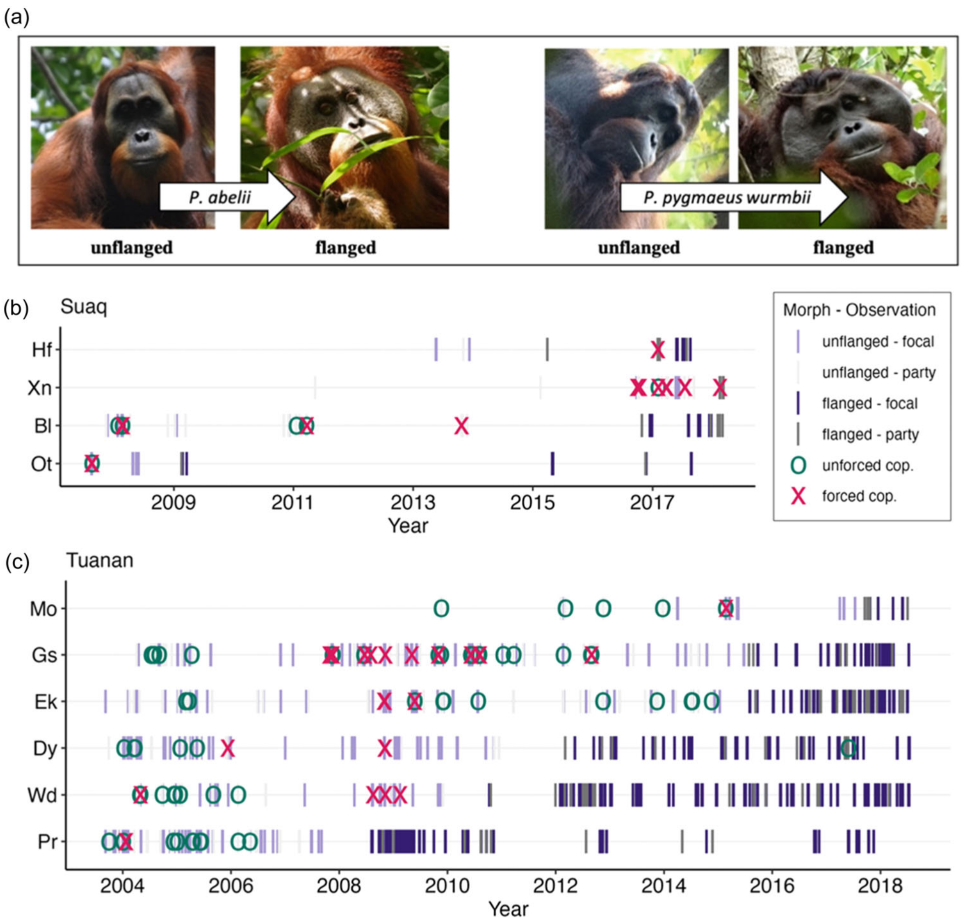

FIGURE 1 Overview of the longitudinal data on males that were observed in both the unflanged and the flanged morph. (a) Pictures of two individuals, one from Suaq (left: Xn; *P. abelii*) and Tuanan (right: Ek; *P. pygmaeus wurmbii*) in their unflanged (left) and flanged (right) morph state (Picture credits [left to right]: C. Schuppli, G. Duvot, A. Marzec, Suwi). (b, c) Timeline (x-axis) illustrating days with focal observations ("-focal") and days when males were observed in association with adult females or males but not as a focal individuals ("-party") by male morph (color) at Suaq (b) and Tuanan (c) and if unforced (*turquoise circles*) or forced (*magenta crosses*) copulations were observed.

reproductive status without measures of female reproductive hormones (Durgavich et al., 2023). Backdating from known or estimated birth dates to conception provides one proxy for the availability of fertile females in the study area (based on orangutans' 8-month-long gestation period: Graham, 1988). We labeled females as *likely fertile* from 1 year before estimated conception and up to the end of the first trimester of pregnancy, i.e., before the onset of pregnancy swellings (Galdikas, 1981). Females were labeled as *unlikely to be fertile* at all other times, unless no birth was documented in the remaining study period, in which case we labeled their reproductive status as *unknown*. Conception events were evenly distributed over the years in both study populations (Figure S1).

2.2 | Behavioral data

At both study sites, long-term behavioral data were collected by well-trained observers during full-day focal follows using the same standardized protocol (https://www.aim.uzh.ch/de/orangutannetwork/sfm.html). To avoid over-habituation and to ensure a broad sample of focal individuals, focal data were collected for, at most, 10 consecutive days per individual with a subsequent break of at least 5 weeks (Figures S1 and S2). Because of their semi-solitary lifestyle, individuals who were not focals were not observed unless they were in a rare association with a focal individual (Table 2). The identities and distances (in classes: ["<50 m", "<10 m", "<5 m", "<2 m", "contact"]) of all individuals within 50 m of the focal were recorded at 2-min intervals. We recorded all occurrences of sexual interactions (Altmann, 1974), but in the current analyses included only sexual interactions with achieved intromission, all failed attempts were excluded (9.7% of all sexual interactions were failed attempts). Copulations were labeled as *forced* if there was any sign of female resistance throughout the sexual interaction. Female resistance behavior could manifest in a/repeated attempt(s) to move away from the male, obstructing the male's attempt to position the female for intromission, slapping and biting the male to evade intromission, and often included the female emitting squeal or scream vocalizations (Fox, 1998; Knott et al., 2010). Forced copulations are an aggregation of different expressions of female resistance. Sample size did not allow us a more fine-grained subdivision, yet this simple classification

TABLE 2 Overview of the total number of copulations and (focal) observation hours during the entire study period (all-occurrence data) by male morph (unflanged and flanged) and study site (Suaq and Tuanan).

Study site	Suaq		Tuanan		Total
Male morph[a]	Unflanged ($N = 46$)	Flanged ($N = 28$)	Unflanged ($N = 37$)	Flanged ($N = 54$)	IDs ($N = 154$)[a]
Total observation hours (focal hours)	2957 h (1529)	2485 h (2179)	8108 h (6749)	17,457 h (16,908)	31,007 h (27,364)
Mean ± *SE* focal follow hours per individual	33 ± 7 h	78 ± 26 h	182 ± 45	313 ± 58 h	
Number of different individuals observed to copulate[b]	$N = 26$[b]	$N = 6$[b]	$N = 25$[b]	$N = 14$[b]	$N = 69$[b]
Forced copulations[c]					
Female resisted	89	3	74	7	173
Unforced copulations[c]					
Female passive	23	10	159	27	219
Female proceptive	2	16[c]	4	4	26
Copulations with unknown female behavior[d]	6	3	15	1	25
Total copulations	120	32	252	39	443

Note: Most analyses in this study include data from male full-day focal follows only, except for variables measured per association hour with females and the proportion of forced copulations.

[a] Total number of individually identified males (longitudinal and cross-sectional data combined). Males from the longitudinal dataset are counted twice, once in the unflanged and once in the flanged morph, therefore the sum of all categories exceeds $N = 154$.

[b] The number of individuals comprises only known males ($N = 69$) who have been observed to copulate (two males from longitudinal dataset, see table footnote a). Many known males have never been observed to copulate despite a large amount of focal follow data (Figure S3).

[c] A total of 13 of the female proceptive copulations involved the locally dominant flanged male at Suaq.

[d] For some copulations, detailed data were missing, often because of visibility constraints (e.g., copulation in a nest) and they could not be attributed to a copulation type.

proved effective to detect conditions in which females are likely to resist (Kunz, Duvot, Willems, et al., 2021). All copulations without apparent female resistance were labeled as *unforced* copulations. The latter also included rare observations of female-initiated copulations, wherein the female initiated the copulation by approaching the male and positioning herself for copulation (Table 2).

2.3 | Ecological data

As a measure of food availability, the monthly Fruit Availability Index (FAI), was included in the analyses (cf. Harrison et al., 2010; Vogel et al., 2017). FAI is the percentage of trees bearing fruits, of monthly surveyed trees (Suaq: ~1000 trees; Tuanan ~1500 trees). Monthly FAIs were available for both study sites over the entire study period. To reflect effects of local variation in FAI, we standardized the values within site using z-transformations ("zFAI"), because the FAIs are generally higher at Suaq than Tuanan.

2.4 | Statistical analyses

We conducted the analyses of individual male behavioral tactics including association, proximity and sexual interaction patterns using two separate, nonoverlapping data sets (i) longitudinal data on males that were observed in the unflanged and flanged morph stage ($N = 10$ individuals [Suaq: $N = 4$, Tuanan: $N = 6$], Figure 1) and (ii) cross-sectional data on males that have been observed in only one morph, either unflanged or flanged ($N = 143$ [Suaq, Sumatra: $N = 66$, Tuanan, Borneo: $N = 77$], Figure S2). For the longitudinal analyses, we assessed behavioral variation over time, with male morph coded as a continuous variable as *years to or since flanged*, whereby time zero marked the first observation of the male with full robust flanges. For the cross-sectional analyses, we assessed behavioral differences between individual males, and male morph was coded as a binary variable, unflanged and flanged. To account for potential within-individual and -morph behavioral changes with age, we added the years since first observation in the study area as an additional factor in the cross-sectional dataset. For both previous data sets, the analyses were conducted based on (i) male full-day focal follow data when assessing individual rates (association, copulation), (ii) a subset of the previous when males were in association with females (proximity) or (iii) any observation day when the male was observed either as a focal individual or as an association partner (copulation frequency, proportion of forced copulations; SI).

We conducted all statistical analyses in R version 4.2.1 (R Core Team, 2022), using the package "glmmTMB" (Brooks et al., 2017) to formulate generalized linear mixed models (GLMMs), and the packages 'coxme' (Therneau, 2018) and "survMiner" (Kassambara & Kosinki, 2018) to construct mixed-effect Cox models (survival analysis). Male identity was included as a random intercept in all analyses, the year and month of data collection were added as nested random factors (~1 | ID/year/month). If variation was limited, i.e., singularity issues showed up, the random intercept was reduced to ~1 | ID (Bolker, 2021). Association time with females was included as an offset term if the model was not exclusively based on full-day focal follows. Models with Poisson and binomial error distribution were tested for over-dispersion (Bolker, 2021; Lüdecke et al., 2021). If data in a model with Poisson or binomial distribution revealed issues of over-dispersion, we conducted negative binomial or beta-binomial GLMMs, respectively (Bolker, 2021). All models were examined for multicollinearity (Variance Inflation Factor <2) and influential cases (Fox & Weisberg, 2018; “DHARMa”: Hartig & Lohse, 2021; “performance”: Lüdecke et al., 2021). We report likelihood ratio tests comparing the full model to the null model containing random intercepts only. Reported absolute ΔAIC values are based on the difference between the null model and the full model, whereby the AIC of the full model was smaller. The pseudo-R^2_c (delta) was calculated using the “MuMIn” package, except for the models with a beta-binomial distribution and mixed-effect Cox models for which the function is not available (Barton, 2018). Second-order interactions to evaluate if behavioral patterns of male morphs might vary as a function of study site, zFAI or time since first observation were tested but are only reported if they improved model fit based on the criteria mentioned above. The model outputs reported in tables show the exponentiated model estimates (“exp. coef.”), the exponentiated 95% confidence intervals (CI), and the z statistics (Wald test statistics) associated *p* values. We highlight results with $p < 0.05$ as significant. Where multiple models for similar hypotheses were run, we highlight results significant after Bonferroni adjustments (association frequency: $p < 0.017$; copulation frequency: $p < 0.025$). All figures were generated using “ggplot2” (Wickham, 2016) and “ggeffects” to illustrate model predictions (Lüdecke et al., 2020). Descriptive statistics are reported as mean and standard deviation for frequencies and as mean and binomial CIs for discrete proportional data (“Hmisc”: Harrell, 2022).

2.5 | Ethical note

Behavioral data collection was noninvasive and exclusively observational. Observers did not interact with the wild orangutans in any way and kept a minimum distance of 10 m to minimize any effect on their natural behavior. The data collection protocol for this study adheres to legal requirements of Indonesia and was approved by the Indonesian State Ministry for Research and Technology (RISTEK), the Directorate General of Natural Resources and Ecosystem Conservation- Ministry of Environment and Forestry of Indonesia (KSDAE-KLHK), the Ministry of Internal Affairs, Indonesia, the Nature Conservation Agency of Central Kalimantan (BKSDA) and Balai Besar Taman Nasional Gunung Leuser (BBTNGL).

3 | RESULTS

3.1 | Association patterns with females—Longitudinal data

For the 10 males known before and after flanging, we found that they were on average in association with more females before than after they had flanged (mean ± *SD*: 0.82 ± 0.76 vs. 0.23 ± 0.48 females per day, *N* = 208 full-day focal follows for unflanged, *N* = 322 for flanged; Table S1). The full model for the number of female associates per full-day focal follow explained significantly more variation than the null model (Table 3). The number of females in association decreased significantly by 9.8% per year over the *years to/since flanged* (Table 3 and Figure 2a). Furthermore, we did not find evidence for variation in the number of female associates with local fruit availability or study site (Table 3). Including second-order interaction terms between either site or local fruit availability and *years to/since flanged* did not improve the model fit. Alternative measures of association frequency, such as association probability and cumulative time spent in association with females, revealed similar patterns (Table S2).

The full model for time spent in proximity (<10 m) to female associates explained significantly more variation than the null model (Table 3). The proportion of association time spent in proximity to females decreased by 11% per *year to/since flanged* (Figure 2b and Table 3). As the number of consecutive days a male spent with a female increased, the proportion of time in proximity to the female increased by 12% per day. We did not find any evidence that the proximity to females varied with the approximate reproductive state of the female, study site, zFAI or the presence of other males (Table 3).

3.2 | Association patterns with females—Cross-sectional data

In the cross-sectional comparison of male morphs, unflanged males had 35% more unique females in association per day than flanged males (Table 4 and Table S1; Figure 2d). The full model for the number of female associates explained more variation than the null model (Table 4). The number of females in association decreased by 6% per year since the individual was first observed. The number of females in association with both unflanged and flanged males was 35% lower at Tuanan than Suaq, albeit this pattern was not significant after Bonferroni adjustment (Table 4). Second-order interaction terms between any study site, male morph, years since first observation or zFAI did not improve the model fit. Besides a higher number of females in association, unflanged males also spent more time in association with females (Suaq: 4.64 ± 5.15 [*N* = 34 days]; Tuanan: 4.91 ± 5.56 [*N* = 169] cumulative hours per day) than flanged males did (Suaq: 1.65 ± 3.70 [*N* = 85]; Tuanan: 0.92 ± 2.83 [*N* = 757] cumulative hours) (Tables S1 and S3).

TABLE 3 Results of the main analyses using the longitudinal dataset of males who developed their flanges during the study period (N = 10).

Response	Variables	Exp coeff	Exp 95% CI	z	p
(a) Number of females in association on full-day focal follow	Intercept	0.23	[0.11, 0.45]	–	–
	ID (N = 10)/year (N = 75)/ month (N = 203)	*random intercept*			
	Site (Suaq vs. Tuanan)	0.92	[0.49, 1.72]	−0.262	0.793
	zFAI	1.12	[0.94, 1.33]	1.289	0.197
	Years to/since flanged	**0.90**	**[0.86, 0.94]**	**−4.521**	**<0.001**
	First observation day with female	**2.54**	**[1.77, 3.65]**	**5.042**	**<0.001**
	Number of consecutive days focal	1.01	[0.94, 1.09]	0.237	0.813
	Poisson GLMM, N = 530 full-day focal follows				
	$\chi^2_{4,9}$ = 69.17, p < 0.0001, ΔAIC = 59.17, pseudo-R^2_c = 0.32				
(b) Proportion of association time in proximity (<10 m) to female associate	Intercept	0.78	[0.24, 2.52]	–	–
	ID (N = 10)/year (N = 50)/ month (N = 91)	*random intercept*			
	Total 2-min bouts in association	*weights*			
	Site (Suaq vs. Tuanan)	1.06	[0.34, 3.33]	0.096	0.924
	zFAI	1.04	[0.74, 1.46]	0.218	0.827
	Years to/since flanged	**0.89**	**[0.83, 0.96]**	**−3.039**	**0.002**
	Additional flanged male present (0/1)	0.64	[0.30, 1.32]	−1.211	0.226
	Additional unflanged male present (0/1)	0.66	[0.33, 1.32]	−1.180	0.238
	Fertility status of female in association				
	Likely vs. unknown	0.56	[0.23, 1.34]	−1.311	0.190
	Likely vs. unlikely	0.65	[0.37, 1.14]	−1.510	0.131
	Number of consecutive female association days	**1.12**	**[1.02, 1.23]**	**2.479**	**0.013**
	beta-binomial GLMM, N = 178 male full-day focal follows with female associates				
	$\chi^2_{5,13}$ = 25.58, p < 0.0001, ΔAIC = 9.58				
(c) Number of copulations on full-day focal follow[a]	Intercept	0.00	[0.00, 0.01]	–	–
	ID (N = 10)	*random intercept*			
	Site (Suaq vs. Tuanan)	0.75	[0.21, 2.43]	−0.470	0.638
	zFAI	1.19	[0.78, 1.68]	0.886	0.376
	Years to/since flanged	**0.87**	**[0.67, 0.89]**	**−3.281**	**0.001**
	z Female association hours (cumulative)	**2.63**	**[2.29, 5.10]**	**7.418**	**<0.001**
	negative binomial GLMM, N = 530 full-day focal follows				
	$\chi^2_{3,7}$ = 95.11, p < 0.0001, ΔAIC = 87.12, pseudo-R^2_c = 0.16				
(d) Number of copulations on association days	Intercept	0.04	[0.02, 0.07]	–	–
	ID (N = 10)/year (N = 92)	*random intercept*			
	log (Female association hours)	*offset term*			
	Site (Suaq vs. Tuanan)	0.59	[0.32, 1.08]	−1.719	0.086
	zFAI	1.10	[0.90, 1.35]	0.918	0.359
	Years to/since flanged	**0.90**	**[0.84, 0.96]**	**−3.009**	**0.003**

TABLE 3 (Continued)

Response	Variables	Exp coeff	Exp 95% CI	*z*	*p*
	Fertility status of female in association				
	Likely vs. unknown	1.03	[0.44, 2.39]	0.059	0.953
	Likely vs. unlikely	0.87	[0.58, 1.31]	−0.666	0.506
	Poisson GLMM, N = 661 male association days[b]				
	$\chi^2_{3,8} = 14.00$, $p = 0.016$, ΔAIC = 4.00, pseudo-$R^2_c = 0.08$				

Note: Type of model, sample sizes, and the likelihood ratio tests comparing the full to the null model (fixed factor = 1; offset term and random intercepts) with ΔAIC and pseudo-R^2_c are reported below the list of fixed factors.

z indicates Wald test statistics and *p* the associated *p* value, whereby the Bonferroni adjusted *p* value for significance for association patterns is $p < 0.016$ and for copulation patterns $p < 0.025$.

Abbreviation: CI, confidence interval.

[a] Adding the presence of unflanged and flanged males on the same day led to convergence errors.

[b] With at least one females (either when males were focal or party member).

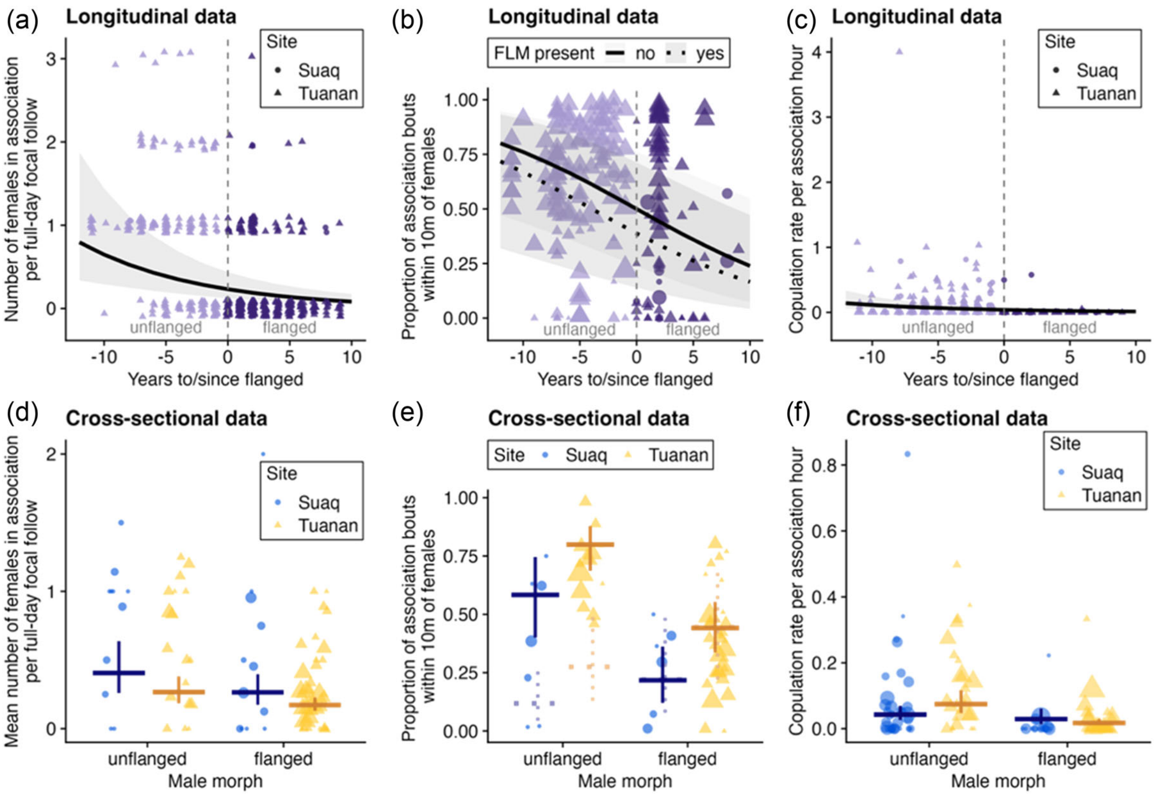

FIGURE 2 Behavioral changes from unflanged to flanged morph: (a–c) Longitudinal data showing the males that have flanged during the study period (*N* = 10) and by years to/since flanged (x-axis); data points illustrate individual full-day focal follow days, a jitter function was applied to make overlaying data points more visible in figure (a). The black line and shaded area show model predictions and upper and lower confidence intervals based on the full model reported in Table 3; (d–f) Cross-sectional data from the two study populations Suaq (*P. abelii*) and Tuanan (*P. pygmaeus wurmbii*); data points are based on individual male means over the entire study period (d: *N* = 80; e: *N* = 55; f: *N* = 111 males) by study site (*color*) and male morph (x-axis), their size is proportional to the number of full-day focal follows composing the data point. The blue and yellow horizontal and vertical lines indicate model predictions and upper and lower confidence intervals based on the model reported in Table 4 (e: The lighter colored model, dashed predictions indicate when an additional flanged male was present during the same day, and the darker color when no additional flanged male was present, respectively).

TABLE 4 Results of the main analyses using the cross-sectional dataset of males who were observed in only one morph stage (either unflanged or flanged) during the study period.

Response	Variables	Exp coeff	Exp 95% CI	*z*	*p*
(a) Number of females in association on full-day focal follow	Intercept	0.52	[0.32, 0.85]	–	–
	ID (*N* = 80)/year (*N* = 212)/ month (*N* = 399)	*random intercept*			
	Site (Suaq vs. Tuanan)	0.65	[0.44, 0.97]	−2.095	0.036
	zFAI	1.08	[0.95, 1.23]	1.200	0.230
	Male morph (unflanged vs. flanged)	**0.65**	**[0.45, 0.93]**	**−2.381**	**0.017**
	Years since first observed	**0.94**	**[0.90, 0.98]**	**−2.688**	**0.007**
	First observation day with female	**2.74**	**[2.10, 3.59]**	**7.379**	**<0.001**
	Number of consecutive days focal	0.98	[0.91, 1.05]	−0.622	0.534
	Poisson GLMM, N = 1045 full-day focal follows				
	$\chi^2_{4,10} = 83.86$, $p < 0.0001$, ΔAIC = 71.86, pseudo-$R^2_c = 0.24$				
(b) Probability of ending an association with females	ID (*N* = 123)/year (*N* = 418)/ month (*N* = 914)	*random intercept*			
	Site (Suaq vs. Tuanan)	**2.23**	**[1.32, 3.75]**	**3.02**	**0.003**
	Male morph (unflanged vs. flanged)	**3.17**	**[2.25, 4.47]**	**6.59**	**<0.001**
	Years since first observed	0.84	[0.68, 1.03]	−1.68	0.094
	zFAI	1.01	[0.97, 1.06]	0.69	0.490
	Mixed-effects Cox model, N = 1203 association days with 231 known endings				
	$\chi^2_4 = 73.28$, $p < 0.0001$, ΔAIC = 49.07				
(c) Proportion of association time in proximity (<10 m) to female associate	Intercept	1.23	[0.52, 2.88]	–	–
	ID (*N* = 55)/year (*N* = 116)/ month (*N* = 159)	*random intercept*			
	Total 2-min bouts in association	*weights*			
	Site (Suaq vs. Tuanan)	**2.84**	**[1.50, 5.37]**	**3.203**	**0.001**
	zFAI	0.94	[0.77, 1.16]	−0.581	0.561
	Male morph (unflanged vs. flanged)	0.20	[0.12, 0.34]	–	–
	Additional flanged male present (0/1)	0.10	[0.04, 0.23]	–	–
	Male morph: Flanged male present	**10.63**	**[2.73, 41.42]**	**3.407**	**0.001**
	Additional unflanged male present (0/1)	1.33	[0.79, 2.25]	1.075	0.282
	Years since first observed	0.95	[0.89, 1.03]	−1.240	0.215
	Fertility status of female in association				
	Likely vs. unknown	0.72	[0.42, 1.22]	−1.225	0.221
	Likely vs. unlikely	**0.46**	**[0.29, 0.73]**	**−3.298**	**0.001**
	Number of consecutive female association days	**1.15**	**[1.02, 1.29]**	**2.288**	**0.022**
	beta-binomial GLMM, N = 282 male full-day focal follows with female associates				
	$\chi^2_{5,15} = 69.07$, $p < 0.0001$, ΔAIC = 49.07				
(d) Number of copulations on full-day focal follow	Intercept	0.01	[0, 0.04]	–	–
	ID (*N* = 80)/year (N = 212)/ month (*N* = 399)	*random intercept*			

TABLE 4 (Continued)

Response	Variables	Exp coeff	Exp 95% CI	z	p
	Site (Suaq vs. Tuanan)	3.78	[0.84, 17.04]	–	–
	Male morph (unflanged vs. flanged)	2.09	[0.37, 11.80]	–	–
	Site: Male morph	**0.10**	**[0.01, 0.67]**	**−2.357**	**0.018**
	Years since first observed	1.00	[0.90, 1.11]	0.057	0.954
	zFAI	1.01	[0.70, 1.44]	0.049	0.961
	z Female association hours (cumulative)	**2.75**	**[2.19, 3.45]**	**8.733**	**<0.001**
	Additional unflanged male present (0/1)	**2.23**	**[1.19, 4.19]**	**2.504**	**0.012**
	Additional flanged male present (0/1)	**2.70**	**[1.3,0 5.64]**	**2.651**	**0.008**
	Poisson GLMM, N = 1045 full-day focal follows				
	$\chi^2_{4,12} = 99.87$, $p < 0.0001$, ΔAIC = 83.87, pseudo-$R^2_c = 0.99$				
(e) Number of copulations on association days	Intercept	0.04	[0.03, 0.07]	–	–
	ID (*N* = 111)/year (*N* = 322)/ month (N = 638)	*random intercept*			
	log (Female association hours)	*offset term*			
	Site (Suaq vs. Tuanan)	1.74	[1.04, 2.92]	–	–
	Male morph (unflanged vs. flanged)	0.68	[0.31, 1.46]	–	–
	Site: Male morph	**0.34**	**[0.14, 0.88]**	**−2.241**	**0.025**
	Years since first observed	1.00	[0.93, 1.07]	0.035	0.972
	zFAI	1.03	[0.85, 1.25]	0.324	0.746
	Fertility status of female in association				
	likely vs. unknown	0.75	[0.46, 1.22]	−1.172	0.241
	likely vs. unlikely	**0.61**	**[0.42, 0.88]**	**−2.597**	**0.009**
	Poisson GLMM, N = 1273 male association days[a]				
	$\chi^2_{4,11} = 33.08$, $p < 0.0001$, ΔAIC = 19.08, pseudo-$R^2_c = 0.06$				
(f) Forced copulations	Intercept	2.77	[1.62, 4.73]	–	–
	ID (*N* = 69)	*random intercept*			
	Site (Suaq vs. Tuanan)	0.12	[0.06, 0.26]	–	–
	Male morph (unflanged vs. flanged)	0.04	[0.01, 0.19]	–	–
	Site: Male morph	**13.48**	**[2.03, 89.5]**	**2.694**	**0.007**
	z Female association hours (cumulative)	0.99	[0.80, 1.22]	−0.100	0.920
	Flanged during study period (0/1)	1.32	[0.57, 3.04]	0.645	0.519
	binomial GLMM, N = 71 male-morph data points				
	$\chi^2_{2,7} = 38.64$, $p < 0.0001$, ΔAIC = 28.64, pseudo-$R^2_c = 0.74$				

Note: Type of model, sample sizes and the likelihood ratio tests comparing the full to the null model (fixed factor = 1; offset term and random intercepts) with ΔAIC and pseudo-R^2_c are reported below the list of fixed factors.

z indicates Wald test statistics and *p* the associated *p* value, whereby the Bonferroni adjusted *p* value for significance for association patterns is $p < 0.017$ and for copulation patterns $p < 0.025$.

Abbreviation: GLMM, generalized linear mixed model.

[a] With females (either when males were focal or party member).

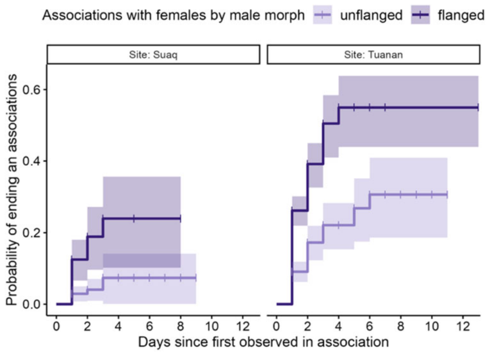

FIGURE 3 Cumulative event plot on the probability of ending consecutive association days with females by study population (left: Suaq; right: Tuanan) and male morph (color). The vertical small lines indicate censored data points. This figure illustrates associations with females from the males' perspective on the total number of consecutive days they have spent with females, independent of female identity.

The probability of ending associations with females on subsequent days was better explained by the full Cox-proportional hazard model than the null model (Table 4). Flanged males were 3.17 (hazard ratio [HR]) times more likely to end consecutive association days with females than unflanged males (Table 4 and Figure 3). Moreover, association days with females were 2.23 (HR) times more likely to be ended at Tuanan than at Suaq (Table 4 and Figure 3). We did not find evidence that the probability of ending an association varied either with zFAI or years since the individual was first observed.

The full model of the proportion of association time spent in proximity (<10 m) to females explained more variation than the null model (Table 4). Compared to flanged males in the same situation, unflanged males remained in proximity to females for a lower proportion of the association time when a flanged male was present during the same day, as the interaction term between male morph and the presence of an additional flanged male indicated (Table 4 and Figure 2e). In the absence of another flanged male, unflanged males remained in proximity to females for a higher proportion of association time than the flanged males. Moreover, the number of association bouts that unflanged and flanged males stayed in proximity to females was 2.84 times higher at Tuanan than at Suaq. Males spent 54% more bouts in close proximity to females that were likely (vs. unlikely) fertile (Table 4).

3.3 | Copulation frequency—Longitudinal data

Males' copulation frequency decreased drastically after they became flanged (Figure 2c), even when we controlled for their reduced total association hours with adult females, i.e., copulation opportunities (Table 3). All 10 focal individuals were observed to copulate with females before flanging, but only three were observed to copulate after having flanged (Figures 1 and 2c). Neither the copulation rates per full-day focal follow nor per day in association with females varied with study site, zFAI or female fertility, but both decreased with years to/since flanged (Table 3).

3.4 | Copulation frequency—Cross-sectional data

Copulations were also rarely observed by males in the cross-sectional dataset. During male full-day focal follows, a total of 64 copulations were observed, 8 at Suaq and 56 at Tuanan. All remaining copulations were observed either during partial-day male focal follows ($N = 63$) or when the female partner was the focal individual ($N = 163$) (Table 2). During full-day focal follows, unflanged males had higher copulation rates than flanged males ($0.014 \pm 0.023\ \text{cop/h}_{\text{focal}}$ vs. $0.003 \pm 0.013\ \text{cop/h}_{\text{focal}}$), and the full model explained significantly more variation than the null model (Table 4). Besides the increased association time with females, males were 2.23 and 2.70 times more likely to copulate on days when additional unflanged or flanged males, respectively, were also in association (Table 4). Further, unflanged males copulated more frequently than flanged males, whereas this difference was more pronounced at Tuanan than at Suaq, as indicated by the significant interaction term between male morph and study site (Table 4).

Unflanged males also exhibited higher copulation numbers per cumulative association hours with females compared to flanged males ($0.105 \pm 0.152\ \text{cop/h}_{\text{association}}$ vs. $0.020 \pm 0.057\ \text{cop/h}_{\text{association}}$). This difference was more pronounced in Tuanan than in Suaq, as the interaction between study site and male morph indicated (Table 4 and Figure 2f). Moreover, male copulation count per cumulative association hour was 39% higher on days when the male was in association with a likely fertile female than on days with a female that was unlikely to be fertile (Table 4).

3.5 | Proportion of forced copulations—Cross-sectional data

On average, males forced 39% (CI = [13, 74]%) of all their copulations (Suaq [$N = 31$]: 61%, CI = [23, 89]%; Tuanan [$N = 38$]: 28%, CI = [8, 63]%). Unflanged males forced a higher proportion of their copulations (44%, CI = [17, 75]%) compared to flanged males (14%, CI = [2, 64]%; Table 2 and Figure 4). This difference between unflanged and flanged males was more pronounced at Suaq than at Tuanan, as indicated by the significant interaction between study population and male morph (Table 4). We did not find any evidence that the proportion of forced copulations varied with the total time spent in association with females (Table 4). Importantly, individual males were observed to have both forced and unforced copulations (Figures 1 and 4). The large majority of unflanged and flanged males who were observed to force all of their copulations (12 of 51 unflanged males; 3 of 20 flanged males) were observed to copulate only once or twice in total (9 out of the 12 unflanged males; 3 out of 3 flanged males). Unflanged males who were observed to copulate at least three times in total ($N = 33$ individuals) forced a mean of 43% (CI = [19, 70]%) of their copulations (Suaq: 74%, CI = [39, 93]%; Tuanan: 29%,

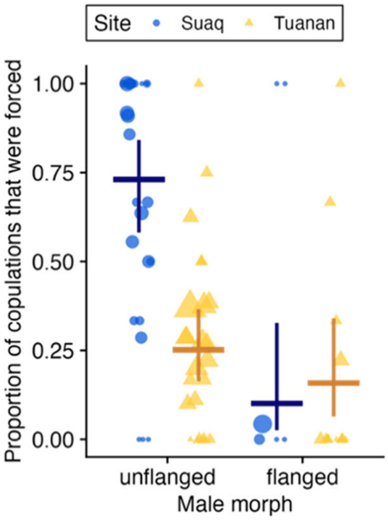

FIGURE 4 Proportion of copulations per individual male that were forced, by male morph (x-axis) and study site (*blue, circles* Suaq [*P. abelii*]; *yellow, triangles* Tuanan [*P. pygmaeus wurmbii*]). Data points (*N* = 71) are based on individual (*N* = 69) and male morph mean proportion of copulations that were forced; data point size is relative to the number of total observed copulations. The blue and yellow horizontal and vertical lines indicate model predictions, and upper and lower confidence intervals based on the model reported in Table 4.

CI = [12, 56]%) and only four of these unflanged males forced all of their copulations, whereas none of the flanged males with 3 or more copulations forced all their copulations (mean 11%, CI = [1, 49]%; Suaq: 4%, CI = [0, 27]%; Tuanan: 17%, CI = [2, 64]%). In sum, few, if any, males forced all their copulations.

4 | DISCUSSION

The extended period of male orangutans' developmental arrest is associated with the behavioral expression of ARTs: both our longitudinal and cross-sectional individual-based findings match previous studies that were cross-sectional and lumped individuals into classes (Table 1). With this more fine-grained analysis, we find that the previously hypothesized difference between Borneo and Sumatra can be more parsimoniously explained. The different behavioral tactics of the unflanged and flanged morph cannot be explained solely by male age, as patterns were consistent across two populations with presumably varying age at flanging (Dunkel et al., 2013) and as we controlled for the time a male was known in the study area. In this discussion we will address the different behavioral tactics of the two morphs, with respect to association patterns, copulation and coercion frequency across the two study populations.

4.1 | Association patterns with females

Long associations of flanged males with females reportedly occur only around the time of conception (Fox, 1998; Schürmann & van Hooff, 1986; Utami Atmoko, Mitra Setia, et al., 2009). Flanged males likely incur higher energetic costs from associating with females compared to unflanged males because of their different activity patterns (van Schaik et al., 2009) and more costly arboreal locomotion (Manduell et al., 2012). Their ability to maintain such associations with females (Kunz, Duvot, van Noordwijk, et al., 2021) therefore depends on the local habitat productivity, which tends to be higher on Sumatra than Borneo (Wich et al., 2011). Rather than persistently pursuing associations, flanged males rely more on their attractivity to females (Knott et al., 2010; Mitra Setia & van Schaik, 2007). In this study, flanged males associated less frequently and hence, appeared to less proactive about both when to associate and with whom (Figure S4; Kunz, Duvot, van Noordwijk, et al., 2021). Although we could not account for reproductive state of all females in the statistical analyses because of missing information for recent years, the data reported here (outliers in Figure 2) are consistent with earlier observations that flanged males were involved in prolonged consortships around the time that these females conceived. Moreover, besides maintaining associations actively (Kunz, Duvot, van Noordwijk, et al., 2021), flanged males also remained in close proximity to likely fertile females, even in the presence of other flanged males (cross-sectional data) and escalated fights are more likely to occur around (fertile) females (Spillmann, 2017). In sum, flanged males associate selectively with females who are likely fertile and appear to mate guard these females in the presence of other males. Thus, their selective, long associations clearly indicate mating effort.

Relative to flanged males, unflanged males spent more time in association with females, and spent a higher proportion of that time in close proximity, for three nonmutually-exclusive reasons. First, associations and close proximity to females may enable unflanged males to monitor females' reproductive state and sexual activities, because female orangutans exhibit neither morphological (Galdikas, 1981; Nunn, 1999; Schultz, 1938) nor behavioral advertisement of the probability of ovulation (Durgavich et al., 2023; Knott et al., 2010). Being tolerated at a distance by flanged males (Mitani, 1985a; Schürmann & van Hooff, 1986) and their relatively high tolerance towards each other (Galdikas, 1985b; Sugardjito et al., 1987) allows unflanged males to avoid the high costs of male-male competition and to eavesdrop on female (proceptive) sexual behavior towards other males during prolonged associations. Second, unflanged male sociality may also serve to establish long-term relationships with females (Utami Atmoko, Mitra Setia, et al., 2009), which may eventually lead to higher reproductive success. Third, sociality of recently dispersed unflanged males may not only serve reproductive strategies but also acquisition of local ecological skills (Mörchen et al., 2023). The observed decrease in female associates with years since first observation in the cross-sectional dataset may provide evidence for the latter two explanations of unflanged male sociality. To conclude, while males appear to decrease sociability with increasing time spent in an area, their association patterns clearly change from the unflanged to the flanged morph.

4.2 | Copulation frequency

Flanged males were observed to copulate less frequently than unflanged males, even when accounting for their overall lower association time. This finding appears counter-intuitive, as available paternity data suggests that siring success is largely skewed towards flanged males (Utami Atmoko, Mitra Setia, et al., 2009). However, the observed copulation patterns may be the result of the interaction between male and female mating tactics. Higher relative siring success of flanged males may result from females approaching long-calls (Setia & van Schaik, 2007; Spillmann et al., 2010) and preferring flanged males as mates around the time of conception (Fox, 1998; Knott et al., 2010; Figure S5). This explains their overall lower copulation rates compared to unflanged males. The exceedingly high copulation (and association) rate of a single dominant flanged male at Suaq is the exception that proves the rule: the majority of these sexual interactions were initiated by the female (Table 2). In contrast, females directed proceptive behavior less often towards unflanged males (Table 2) and unflanged males may therefore initiate mating during periods when females are less likely to be fertile (Figure S5). All in all, our observed higher mating rates during the unflanged state likely do not translate into siring success but suggest a "best-of-a-bad-job" tactic. The lack of observed copulations by some flanged males in our longitudinal dataset likely indicates that we did not capture the relatively brief periods when males were in association with a peri-ovulatory female.

4.3 | Proportion of forced copulations

The highly variable coercion rate among different males (Figure 4) indicates that forced copulation is a variable male mating tactic, which is in accordance with increased rates of resisted copulations in the context of male-male competition (Kunz, Duvot, Willems, et al., 2021) and negative female preference (Knott et al., 2010). Thus, although females were more likely to resist mating attempts by unflanged than by flanged males, sexual coercion is not the default strategy of unflanged males. Unflanged males did not force all their copulations, nor did flanged males refrain from forcing copulations in all contexts. The higher proportion of copulations that were forced in the Suaq population compared to Tuanan is consistent with higher population density and a larger number of males competing for access to females (Knott, 2009; e.g., *Pan troglodytes*: Watts, 2022).

Contrary to both our prediction and previous studies, we did not find evidence for higher coercion rates among flanged males in Borneo (Tuanan) than Sumatra (Suaq), despite evidence for more direct contest competition among flanged males at Tuanan than at Suaq (injuries resulting from physical fights [Dunkel et al., 2013]; confrontational assessment [Spillmann, Willems, et al., 2017]). First, flanged males may choose timing or contexts in which female resistance is less likely, resulting in lower copulation rates. Moreover, female resistance is overall less likely toward dominant males (Kunz, Duvot, Willems, et al., 2021). Second, our individual-based approach meant that half of all observed forced copulations (5 of 11) at Tuanan and one-third (1 of 3) at Suaq by unidentified flanged males were excluded from the analyses. If we were to lump individuals into morph classes, like previous comparative studies (Knott, 2009; Utami Atmoko, Mitra Setia, et al., 2009; Utami Atmoko & van Hooff, 2004), flanged males' forced to unforced copulation ratio would be lower at Suaq (9%, $N = 11$) than at Tuanan (24%, $N = 46$) (Table 2). Indeed, the fact that unknown flanged males encounter more female resistance may be informative, since they were presumably visitors to the study area and not regularly present compared to other flanged males (Knott, 2009; Mitani, 1985a; Spillmann, 2017). If there is a risk of infanticide in orangutans (Knott et al., 2010; Scott et al., 2019), females may be more reluctant to mate with visitor or clearly subordinate males in vicinity of resident males, as this may reduce the paternity certainty of the latter to the disadvantage of the female and her (future) offspring (Kunz, Duvot, Willems, et al., 2021; van Schaik et al., 2004). Third, periods of unstable male dominance relationships may lead to different female-driven mating patterns (Utami Atmoko, Mitra Setia, et al., 2009; Utami Atmoko & Mitra Setia, 1995). The Suaq orangutan population had a period of such instability from 2014 to 2018. In our sample, the former dominant flanged male was still an outlier with high association and copulation frequencies and low coercion rates, confirming previous studies that found low copulation rates, and hence no forced mating, by dominant flanged males (Fox, 2002). For now, we conclude that flanged male mating competition is pre-copulatory, contest-based, and likely relies on female choice.

5 | CONCLUSION

Male orangutans are unique among primates, and mammals in general, in that they exhibit irreversible bimaturism combined with a variable, extended period of developmental arrest. The results of this study provide the first quantitative longitudinal analyses of individual males who were observed during both morph states. Our results confirm the presence of sequential ARTs of the two orangutan male morphs in two populations, as proposed by previous studies. Although these tactics also show variation within male morphs, we conclude that unflanged males appear to follow a different mating tactic, consistent with a "best-of-a-bad-job" scenario (Dawkins, 1980): they avoid direct contest competition, but can hardly rely on female choice. The unique orangutan male ARTs have likely evolved through a combination of their remarkably low adult mortality (van Noordwijk et al., 2018), concealed ovulation (Knott et al., 2010; Nadler, 1981), and siring opportunities that are scattered in time and space (Pradhan et al., 2012).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and source code for the analyses reported in the main text of this manuscript are available on the Harvard dataverse repository: https://doi.org/10.7910/DVN/UMRGZC.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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