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Research Article

Behaviour of Wild, Non-Adult Bornean White-Bearded Gibbons (*Hylobates albibarbis*) in Indonesia

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ABSTRACT

Primates have an extended juvenile period associated with critical social and environmental learning. In particular, social play is positively associated with brain size in primates, indicating an important role in cognition and development. However, this behaviour has been overlooked in the Hylobatidae family. The activity patterns of eight non-adult Bornean white-bearded gibbons (*Hylobates albibarbis*) from four groups were studied in the Sebangau peat-swamp forest in Borneo from 2005 to 2019. We compare our findings to previous reports for adult conspecifics, report the directionality of non-adult play behaviour, and examine whether the weather impacts daily activity patterns. Feeding (39.5%), resting (27.6%) and travelling (23%) were the main activities of juveniles, while infants mostly played (42.1%) or clung to their mothers (38.3%). Non-adult groups socialised and observed their surroundings more often, and they travelled and called less often than adults. Feeding and resting frequency did not differ significantly from that of adults. Infants engaged in self-centred play twice as often as juveniles and directed most of their playing attention towards sub-adults (58%). Weather variables, previously reported to be good predictors of certain adult activities, such as singing, did not appear to affect infant and juvenile activities. Play is a critical part of primate physical and social development, and this study describes some key behaviours of young gibbons. Understanding the play behaviour of gibbons in the wild will help inform the rehabilitation of an ever-increasing number of orphaned individuals who are victims of the illegal pet trade.

1. Introduction

The often complex structure of primate societies reflects the species adaptive response to resource availability, mating strategies, and predator avoidance, and, therefore, its study can inform the design and implementation of targeted conservation strategies (Fuentes 2007; Strier 2007). Since a species can demonstrate a degree of behavioural plasticity in response to its habitat, it is important to study species' behaviour in multiple habitats using methods that can detect behavioural adaptations to them. Activity budget is such a method, which has been widely employed by primatologists worldwide (e.g. Isbell *et*

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al. 1999; Cheyne *et al*. 2008a; Hockings *et al*. 2012; Russon *et al*. 2015).

The Bornean white-bearded gibbon (*Hylobates albibarbis*) is an IUCN Red List Endangered ape endemic to Kalimantan (Indonesian Borneo) south of the Kapuas River and west of the Barito River (Cheyne 2010a; Cheyne *et al*. 2016). It occurs in a range of evergreen tropical forests (primary, secondary, selectively logged), and habitat loss is the primary threat to the species (Marshall *et al*. 2020). Existing behavioural studies have focused on the activity budget of adult rather than non-adult (infant/juvenile/sub-adult) individuals (Marshall and Leighton 2006; Marshall *et al*. 2009; Singh *et al*. 2018; Cheyne *et al*. 2010b)-a trend in primate behavioural studies (Oliveira *et al*. 2003; Hayaki 1985).

In this study, we use activity budgets to examine the behavioural ecology of wild, habituated, non-adult Bornean white-bearded gibbons (*Hylobates albibarbis*) in a degraded peat forest within Sebangau National Park (Page *et al*. 1999). The peat-swamp forest is a threatened habitat type due to pressure to extract commercially valuable products such as timber, conversion to farmland, and very low levels of protection (Haag 2007; Hamard *et al*. 2010; Cheyne *et al*. 2016). We compare our findings to previous reports for adult conspecifics. Moreover, we examine the directionality of play behaviour since play constitutes an important part of the daily activities of primates, strengthening group relationships and training, especially juveniles, in important life skills (Barret *et al*. 1992; Strier 2007). Play can be affected by various factors, including sex, species, tree height and possibly weather conditions.

We commenced our study, aiming to test the following four hypotheses. Firstly, we hypothesised that non-adult gibbons' activity budget would differ from adults within the same group. Secondly, based on observations of other gibbon species (Cheyne 2009; Inoue *et al*. 2016), we hypothesised that there is spatial (vertical) variation in where play occurs based on the age of a gibbon. Specifically, we anticipated a positive correlation between the height of play and the gibbon's age group - i.e., older gibbons will play higher in the canopy than younger ones. Thirdly, we hypothesised that adverse weather conditions would affect play frequency. Specifically, rain would negatively affect play (Cheyne 2008a). Lastly, we hypothesised that play would occur more frequently during the late morning and noon hours (~0900h-1200h) than other periods of the day, reflecting the activity budgets of adult gibbons who rest and socialise more during the middle of the day (Cheyne 2010a).

2. Materials and Methods

2.1. Study Site

The study was conducted within a 9 km^2 area (2.345° S, 114.036° E) of the Natural Laboratory of Peat-Swamp Forest (NLPSF), which is part of the Sebangau National Park (5,300 km^2) in the Indonesian Province of Central Kalimantan (Figure 1). The area contains one of the most extensive tracks of peat-swamp forest in Kalimantan, is characterised by deep peatland and low elevation, and is thought to be home to the largest population of the Bornean white-bearded gibbon (Page *et al*. 1997, 1999; Morrogh-Bernard *et al*. 2003; Cheyne 2010a). The study area is secondary, seasonally flooded (October-June), closed canopy, and evergreen forest, with logging taking place before 2002. The mean annual temperature is 26°C, and the average annual rainfall is 2,320 mm (Cheyne 2010a; Harrison *et al*. 2016; Harrison *et al*. 2010).

We have detailed information about population density and the number of gibbons in Sebangau National Park (Cheyne *et al*. 2008b; Cheyne *et al*. 2016b). However, illegal logging, habitat conversion, and hunting for the pet trade are threats to gibbons throughout their range, though no specific data on potential population decline are available for this area (Singh *et al*. 2018; Campbell *et al*. 2015; Cheyne *et al*. 2016a; Marshall *et al.* 2020). In addition to *H. albibarbis*, Sebangau is home to nine species of primates, including the Critically Endangered Bornean orangutan *Pongo pymaeus* wurmbii.

2.2. Data Collection

Data were collected from 2005-2019 (primate follows ceased in April 2020 due to COVID-19 (Santos *et al*. 2020). We observed the behaviour of six sub-adults (>4 years), two juveniles (2-4 years old) and four infants (0 -24 months old) gibbons from three groups previously habituated by Cheyne (2010a) to study the behaviour of the adult gibbons (Table 1) using an established ethogram (Supplementary Table 1). Due to the length of the study, some individuals were observed over several years and thus fall into different age classes. Non-adult gibbons were not the main focus of this study over the whole period from 2009-2020, thus the tiny sample size for each non-adult over the length of the study.

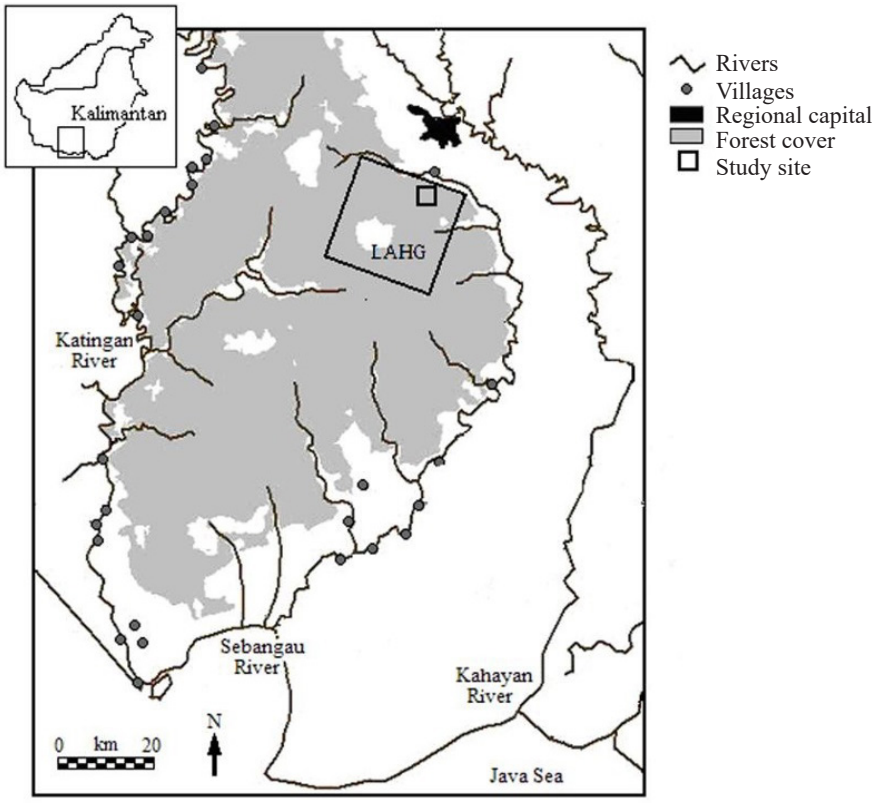

Figure 1. Location of the national laboratory of Peat-Swamp Forest (LAHG-laboratorium alam hutan gambut) and the study area within the Sebangau National Park

Table 1. Breakdown of study animals in this study: group, age, sex, number of data days and data collection dates

Name	Group	Age class	Sex	Number of full follow days (this study)	Year(s) when data collection took place
Chilli (C)	C	Infant	M	50	May-August 2009
Jet Li (K)	K	Infant	F	47	May-August 2009
Elen Li (K)	K	Infant	F	67	September 2016-2017
Nidji (N)	N	Infant	M	36	May-August 2009
Chilli (C)	C	Juvenile	M	50	May-August 2014
Jet Li (K)	K	Juvenile	F	50	May-August 2014
Cynthia (C)	C	Sub-adult	F	25	May-August 2009
Chilli (C)	C	Sub-adult	M	67	September 2018-2019
Zhang Ziyi (K)	K	Sub-adult	F	49	May-August 2009
Jet Li (K)	K	Sub-adult	F	57	September 2016-2017
Nina (N)	N	Sub-adult	F	30	May-August 2009
Neo (N)	N	Sub-adult	M	30	May-August 2009

The fact that almost no same-age playing was observed was also to be expected since, like all Hylobates species, the white-bearded gibbon is socially monogamous, and females typically give birth to single young. A typical social unit, therefore, consists of a breeding pair of adults and their offspring of different ages (sub-adult, juvenile, infant, depending on the female's reproductive history).

Age classes were ascribed using standard age/growth rates for gibbons (Cheyne 2007, 2009). A standardised five-minute instantaneous sampling protocol was used to record the behaviour (Altmann 1974) of one focal animal per day. The data was collected by teams of two researchers, occasionally a third member joining the team for training purposes.

The data collection protocol was identical to Cheyne (2010a). Gibbon groups were located in sleeping trees before they awoke and followed throughout the day until entering the afternoon/evening sleeping tree. The

average follow day length was 8-10 hours (starting around 0430 hours and finishing around 1500-1600 hours). Once a group was located, the team maintained a minimum distance of 10-15 m from the selected focal animal. When the focal animal was out of sight, the research team recorded this fact at the five-minute interval and tried to relocate the animal. The daily travel path of the focal animal was recorded using a handheld GPS unit while following the gibbons' path and recording waypoints points of interest, e.g., trees where the gibbons stopped to feed, rest, and socialise.

The gibbon ethogram used was developed by Cheyne (2010a). It differentiates between 11 primary activities and, for four (calling, clinging, socialising, playing), 15 secondary sub-categories (e.g., primary: calling, secondary: alarm calling; Table 1). When play behaviour involved interaction among two or more gibbons, the age group and sex of the initiator and the receptor(s) were also recorded. We recorded the focal animal's position in the tree concerning the height of the tree (in five-minute intervals), as well as the daily minimum and maximum temperature (°C) and precipitation (mm). Weather variables were measured at the base camp using a thermometer and precipitation gauge.

2.3. Data Analysis

The behavioural observations were summarised across age groups developing sub-adult, juvenile and infant activity patterns that are comparable with Cheyne's (2010b) adult gibbon data (collected at the same time as part of another study). "Lost" and "unknown" records were excluded from the activity, as we assumed that there was no bias among individuals. Because only a tiny portion of observations were recorded as "other", it was decided to exclude them from the analysis. A play bout refers to any occurrence of play within a five-minute interval (the instantaneous sampling interval for this work) (Cheyne 2010a; Altmann 1974).

We limit our report on infant gibbon behaviour to descriptive statistics since the small number of study animals (n=2) did not permit further analysis. In the case of juvenile gibbons, we used general linear models to examine whether there was significant variation in the frequency of each type of their behaviour (primary or secondary) to that of adult gibbons. As there was a monotonic relationship between tree and play height, Spearman's rank correlation (rs) was used to evaluate correlation and an independent t-test was used to evaluate seasonal differences. Pearson's chi-square was used to test the hypothesis that the time of day affected play height.

We calculated the mean daily distance travelled by each animal using the coordinates recorded in the field and based on the length of the follow for all groups, as per the observations of Cheyne (2010a). Finally, we examined the potential effect of weather variables on the frequency of every type of behaviour. All statistical analyses were conducted using the open-source statistical software R (v. 2.14.1), with a significance level of 5%. Geospatial analysis was undertaken using Quantum GIS open-source software (v. 1.7.4).

3. Results

3.1. Activity Budget

3.1.1. Primary Activities

Overall, juvenile gibbons spent most of their time feeding (39.5%), resting (27.6%) and travelling (23%), while infants played (42.1%) and clung to their mothers (38.3%) (Figure 2). We did not observe aggressive behaviours in either of the three age classes. There was no significant difference among juveniles in the proportion of their time engaged in each behaviour compared to infants, except for resting (ANOVA, $F_{5,16}=3.99$, $p=0.01$; 27.61±19.05%) and play (ANOVA, $F_{4,14}=2.89$, $p=0.01$; 28.43±17.16%).

Non-adults were observed, "playing" (Wilcox sum rank test, $W=0$, $p<0.001$, $\bar{x}JUV=6.7\%$, $\bar{x}AD<0.1\%$), "socialising" ($W=11$, $p<0.001$, $\bar{x}JUV=1.7\%$, $\bar{x}AD=0.2\%$), "feeding" ($W=18$, $p=0.001$, $\bar{x}JUV=39.8\%$, $\bar{x}AD=23.4\%$) and "observing" ($W=35$, $p<0.001$, $\bar{x}JUV=0.7\%$, $\bar{x}AD=0\%$) more frequently than adult gibbons, and "travelling (being on the move)" ($W=197$, $p<0.001$, $\bar{x}JUV=23.5\%$, $\bar{x}AD=43\%$) and "calling" ($W=195$, $p<0.001$, $\bar{x}JUV=0.8\%$, $\bar{x}AD=16.5\%$) less frequently (Figure 3).

Play-related activities also differed in their frequency between infants and juveniles and sub-adults (Figure 4), with the former spending most of their playing time in self-centred activities (e.g., "pottering" the tree, swinging from the branches) and the latter in more interactive activities (e.g., chasing and wrestling).

3.2. Directionality of Play

When infants initiated playing, they most often directed their play to sub-adults (58%) and juveniles (34%), whereas juveniles directed their play primarily to sub-adults (68%) (Figure 5).

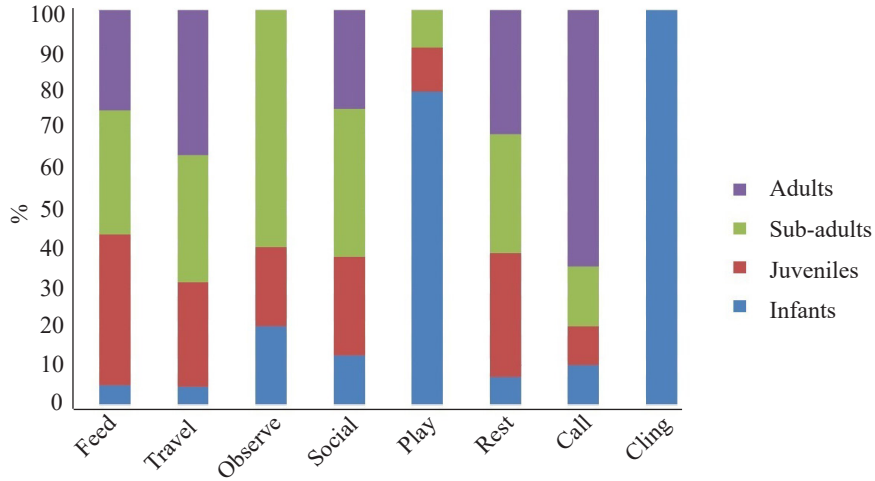

Figure 2. Relative frequency of primary activities of infant (n=2), juvenile (n=4), sub-adult (n=6) and adult (n=12) (Cheyne 2010; n=24) *Hylobates albibarbis* in the study area

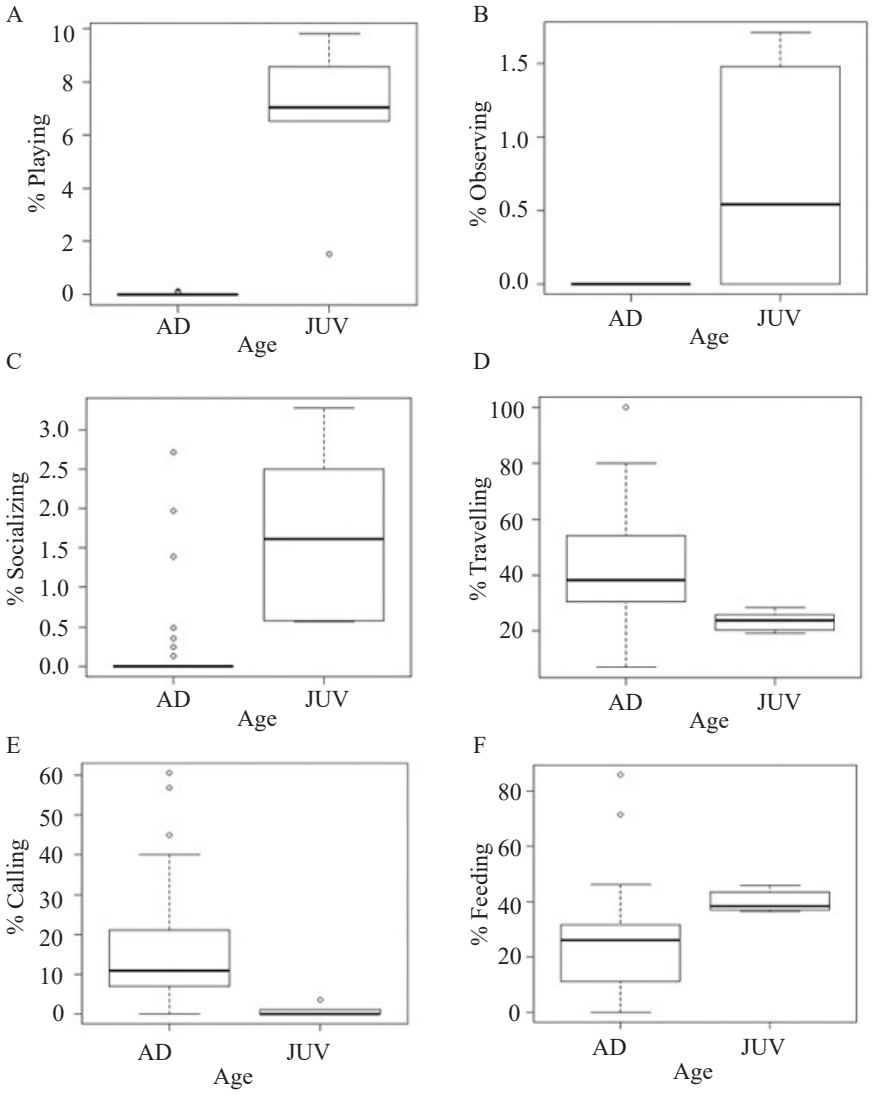

Figure 3. Occurrence per age category (AD=Adult, JUV=Non-adult) of six key behaviours from this study: a) "Playing", b) "Observing", c) "Socialising", d) "Travelling", e) "Calling" and f) "Feeding"

3.3. Play Height

The mean height for all play was 14.83 m (range=1-23 m, SD=3.99 m). All non-adult gibbons had a mean play height of 14 m (n=82, range=8-23 m), and the adult's average play height was 15 m (n=52, range=8-23 m, Table 2). Tree height mean was 16 m (range=8-28 m, Table 2). There was a positive correlation between tree height and play height (N=138, rs=0.810, P=0.00).

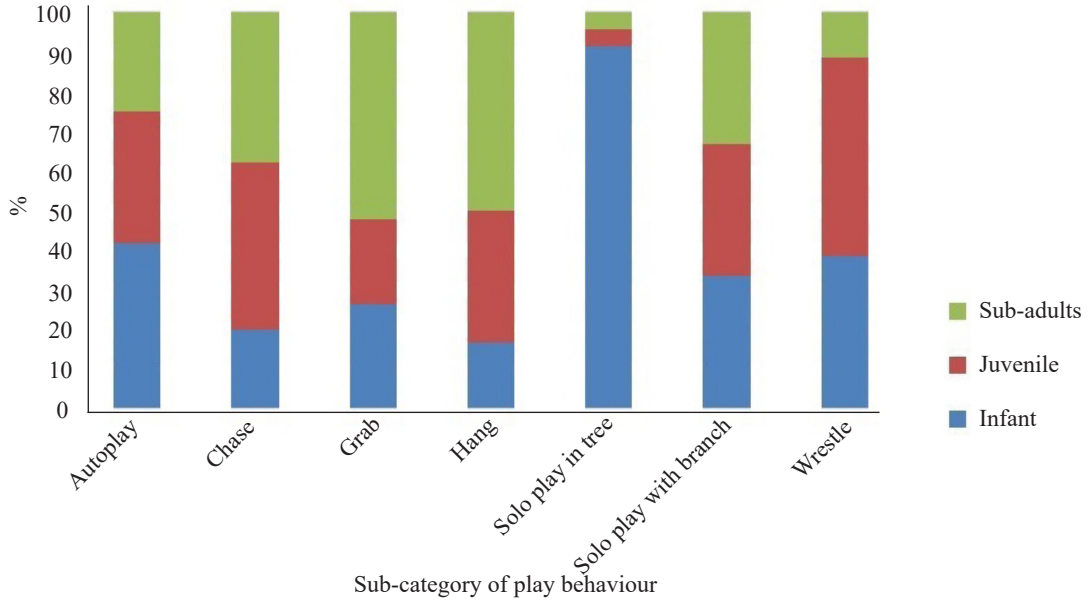

Figure 4. % of time engaged in playing sub-category activities

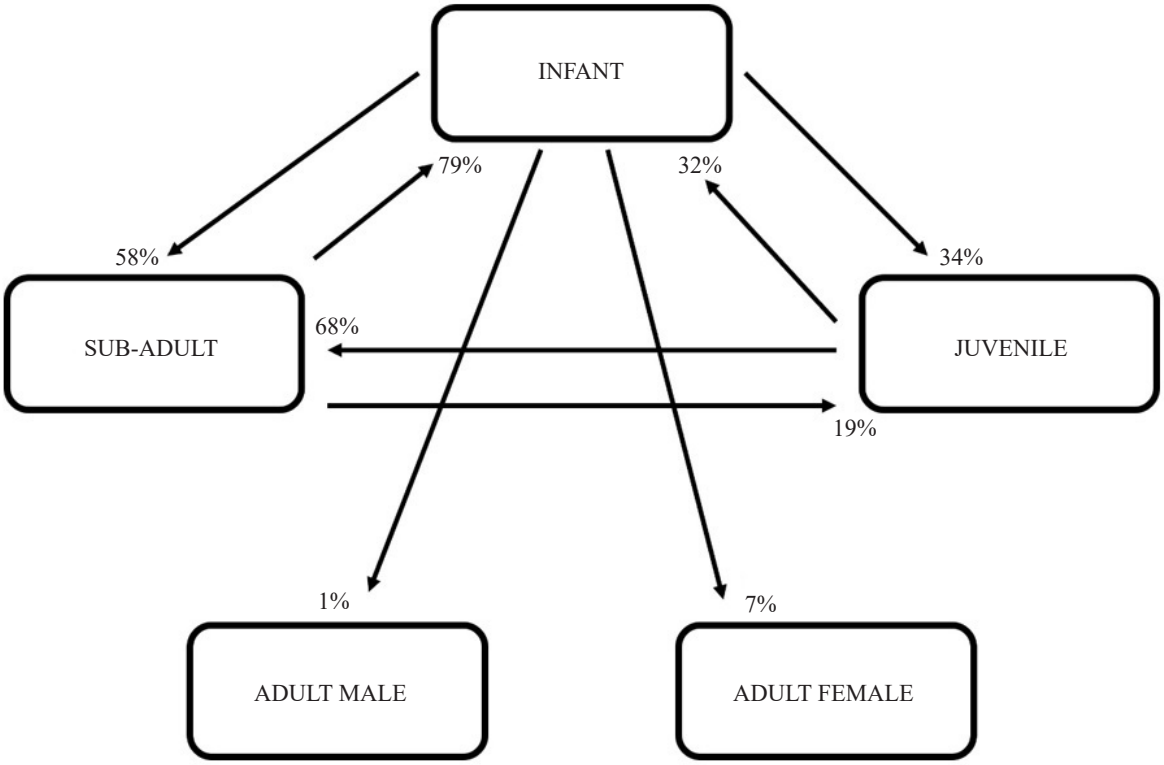

Figure 5. Directionality of the play in *Hylobates albibarbis*. The arrows show the direction of the activity (initiator to receptor), and the numbers represent the frequency at which the direction of play initiation was observed

3.4. Weather Influence on Activity Budget

Although daily temperature range, mean daily temperature and rain level were good predictors of some infant and juvenile behaviour frequencies (Table 3), we did not observe any overarching trends across behaviour types and the two age groups. Other than that, all the gibbons rested significantly more during rain. The daily temperature range was also a significant predictor of "play" frequency for juvenile and infant gibbons but with an inverse relationship. Infants were likely to play more on days with higher temperature ranges, unlike juveniles, which were less likely to do so.

4. Discussion

Among mammals, primates, especially apes, have an exceptionally long juvenile period (Joffe 1997). This is a formative, vulnerable life stage when young animals acquire survival and social skills (Kaplan *et al.* 2000; Bolter & Zihlman 2002, 2007). However, despite the importance of this period for primates, non-adult primate behavioural ecology is less studied than adults, especially in the wild and for endangered species such as the Bornean white-bearded gibbon. Studies such as this one are especially timely considering the pressure under which peat-swamp forests are in Kalimantan and the important flagship role that gibbon (along with orangutans) conservation can have in protecting this habitat type.

4.1. Activity Budget

Juvelines were engaged in substantially more play behaviour than adults, including self-play with objects (twigs and leaves), chasing, jumping and wrestling, and initiating play with other individuals (adult and non-adult) through slaps and poking with hands. These varied behaviours demonstrate the complexity of gibbon play and highlight the importance of solo play and play with other individuals. A comparison of the differences in play style between a juvenile white-bearded gibbon and an orangutan (*Pongo pygmaeus* wurmbii) recorded in the Sebangau National Park can be viewed here. The almost inverse relative frequency with which non-adult animals in this study were observed feeding and travelling compared to adults from Cheyne's (2010b) study warrants closer examination. One possible explanation could be that adult data were combined (male and female) and that adult males travel farther than adult females as they range wider to patrol the territory, whereas adult females take a more direct route between feeding/resting sites (Savini *et al*. 2008; Asensio *et al*. 2010; Inoue *et al*. 2016). Compared to

Table 2. Play bouts for *Hylobates albibarbis* by age and sex with height range of play and tree height. Adult play data from Cheyne (2010)

Age category	Sex	Number of bouts	% of bouts	Mean play height (m)	Min. play height (m)	Max. play height (m)	Mean tree height (m)	Min. tree height (m)	Max. tree height (m)
Adult	F	40	29.9	16.4	8	23	18.4	8	28
Adult	M	12	8.9	12.7	8	18	15.5	13	23
Sub-adult	F	6	4.4	16.3	13	18	18.8	18	23
Juvenile	F	52	38.9	13.6	8	23	14.8	8	23
Infant	F	24	17.9	15.9	13	18	16.9	13	23
Total		134	100	14.8	8	23	16.5	8	28

Table 3. List of models considered to evaluate the influence on the activity budget of non-adult white-bearded gibbons, with a p-value lower than 0.05(*)

Age	Weather	Behaviour	r^2	F	Df	p-value	Relation
Infant	Temperature	Calling	0.42	4.37	1.6	NS	+
		Playing	0.46	5.04	1.6	*	+
		Unknown	0.83	29.59	1.6	*	-
	Mean	Clinging	0.57	7.93	1.6	*	+
		Resting	0.54	7.13	1.6	*	-
	Rain level	Resting	0.85	34.05	1.6	*	+
		Travelling	0.66	11.78	1.6	*	+
Juvenile	Temperature	Playing	0.36	11.5	1.20	*	-
		Resting	0.24	6.50	1.20	*	+
	Mean	Feeding	0.15	3.61	1.20	NS	-
	Rain level	Calling	0.92	247.4	1.20	*	+
		Resting	0.29	8.08	1.20	*	+

the activity pattern of adult gibbons in the same area Cheyne (2010a), the non-adult gibbons of this study differed significantly in the relative frequency of all primary behaviours except "resting".

The reported differences between juvenile and adult gibbons in the relative frequency of other behaviours were unsurprising. The juvenile gibbons' limited time (1%) spent calling compared to adults (9%) reflects their non-developed singing skills, which are perfected around 4 years old when they start joining singing duets (Geissmann 1984; Cowlishaw 1996; Clarke *et al*. 2006). However, the proportion of juvenile time spent in behaviour involving social interactions can be compared to that of other gibbon species. This study's juvenile gibbons spent 8.4% of their time interacting with other group members ("socialising" + "playing"), which is within the relative frequency range reported for mixed–age group white-handed gibbons (>10%, Bartlett 2003) and Javan gibbons (6%, Kim *et al*. 2011). Of course, we need to consider the short duration of this study and the possibility that social interactions may display seasonal patterns in their frequency. From our long-term data, we do not see significant differences in frequency or type of play based on season, nor any substantial difference in play types as the individuals age. What does change with age is the frequency of play activity. Such seasonality has, for instance, been reported previously by Fan *et al*. (2008) for Nomascus concolor and Cheyne (2010a). Moreover, given that the adult white-bearded gibbons socialised half as frequently (~4%) during Cheyne's study and that Kim *et al*. (2011) and Bartlett (2003) did not differentiate between adults and non-adults, it is very likely that the above activity budget differences are less inter-specific and more intra-specific and intra-generational as has been found for gelada baboons (Barret *et al*. 1992).

4.2. Directionality of Play

The younger gibbons within a group generally directed their play attempts to older individuals, and the younger gibbons initiated the majority of play bouts. Sub-adult gibbons were the least likely to initiate a play bout (Mendonça *et al*. 2017). The activity budget of the infant gibbons, although from only four animals, clearly shows their dependence on their mother primarily, followed by siblings and then the adult male. In other primate species, especially group-living ones, there is more play between similarly aged individuals as there are more youngsters in the group (Hayaki 1985; Lewis 2000). This is expected as infancy is a vulnerable period for primates, and mothers are responsible for providing food and protection and teaching them how to safely explore their environment (Bolter and Zihlman 2007). These findings are similar to those of other primates, where play frequency diminishes with age (i.e., the individual initiates play less) but will still engage in play if another individual initiates this.

4.3. Play Height

Sub-adult gibbons played at an average height higher than younger gibbons. Neither sub-adults nor infants were seen to approach the ground (0-10 m), unlike juveniles who did (Asensio *et al*. 2010). This suggests that infant gibbons are perhaps less cautious, and sub-adults are more confident to play higher in the canopy (Inoue *et al*. 2016; Neha *et al*. 2021).

4.3. Weather Influence on Activity Budget

Previous studies have examined the potential effect of weather on gibbon activity budgets on a seasonal level but not on a daily one as in this study. For example, Kim *et al*. (2011) found that seasonal variation in rainfall and temperature levels did not affect Javan gibbon activity budgets. Among the significant relationships found between behaviour frequencies and weather parameters in this study, only two were significant ($r2>0.75$) - rain level and juvenile calling and rain level and infant resting. An effect of rain on adult white-bearded gibbons' calling frequency was also reported by Cheyne (2008a) at another peat-swamp forest site. As information on the nature of these calls was not recorded, it is impossible to interpret these patterns. It is nevertheless helpful to note the potential role that weather can have on this species' behaviour, at least for some age groups and activities.

4.4. Play

This study's findings on gibbon play are especially valuable, as few wild gibbon studies examine play and even fewer report its directionality. The markedly higher proportion of time that non-adult gibbons spent playing compared to adults was expected. In most primates, play decreases with age and is typically associated with infants and juveniles (Lewis 2000; Palagi 2006). Infants played five times more often, engaged in more self-play, and directed some of their playing to adults, including their mothers, compared to juveniles. This is not surprising as juveniles-more

independent than infants-spent six times as much time travelling and feeding.

The oldest offspring in the groups were sub-adults (<8 years old), who both received and directed play to infants and juveniles. One benefit of accepting sub-adult animals in the nucleus of their natal group, rather than having them live in the group's periphery, is that they may serve as valuable play partners to their young siblings (Brockelman *et al*. 1998). Our findings support this theory. Due to the limited number of studies on gibbon play (wild or in zoos or rescue centres), comparisons are hard to make across other populations of *Hylobates albibarbis* or other gibbon species. Inoue *et al*. (2016) did find some similarities in behaviour reported here for *Hylobates funereus*.

The relative brevity of the study periods on each focal gibbon limits the confidence to generalise the behavioural ecology of non-adult white-bearded gibbons throughout the year. However, the findings presented here certainly bring attention to examining the behavioural ecology of all age groups. Similar studies must be undertaken over multiple seasons and in sites with different habitats or anthropogenic disturbance/habitat degradation levels. Given the current pressure levels on Borneo's peat-swamp forests, the white-bearded gibbon will have to persist in an increasingly human-dominated landscape if it is to survive. Therefore, a good understanding of the species' behavioural ecology is imperative for understanding the full impact of threats, such as the illegal hunting of gibbons for the pet trade-and resource management decisions, such as the extent, timing and species of selective logging.

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Supplementary Material

Supplementary Table 1. Gibbon ethogram used in this study (Cheyne 2010)

Behaviour	Description	Secondary behaviour
Calling	Calls, or tries to call if the focal animal is non-adult	Alarm calling
		Crying
		Singing
Clinging	Attached to the mother	Mother feeding
		Mother resting
		Mother travelling
Socialising	Grooming with other group members	Allo-grooming
		Grooming
Playing	Displaying playing behaviour (conspecific interactions are non-aggressive and exclude grooming	Auto-play
		Chasing other individual
		Grabbing an object
		Hanging from branch
		Pottering the tree
		Play with branch
		Wrestling with other individual
Feeding	Actively foraging or chewing food (excludes infant breastfeeding)	
Resting	Lying or sitting in a tree, without engaging in another behaviour	
Travelling	Moving from one point to other	
Observing	Observing the behaviour of other group member(s)	
Aggression	Calling aggressively to other individual(s)	
Other	Observed behaviour does not fit in any of the categories mentioned above or is not possible to determine	
Lost	Focal individual was out of sight	