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Transient co-singing of offspring and mothers in non-duetting Javan gibbons (*Hylobates moloch*)

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While the vocalizations of non-human primates were thought to be innate, recent studies have revealed highly flexible vocalizations in immatures. This behavior suggests that social influences have an important role in developing vocalizations. Yet not much is known about how non-human primate vocalization develop and how the vocalizations of immature animals differ between sexes. Here, we analyzed 95 cases of co-singing between mothers and offspring out of 240 female songs from three groups of wild Javan gibbon (*Hylobates moloch*) in Gunung Halimun-Salak National Park, Indonesia, between 2009 and 2021. *Hylobates moloch* is one of only two gibbon species with pairs that do not duet. Instead, they produce sex-specific solo songs. We found that both offspring female and male *H. moloch* follow their mothers' female-specific songs, similar to other duetting gibbon species. Immatures started co-singing with their mothers from 7 months old, but with an average starting age of about 24 months. As female offspring grew older, they co-sung with mothers more often while male offspring did not. After 7 years of age, both sexes stopped co-singing with their mothers and started singing alone, following their own sex-specific vocalizations. We did not find any relation between male offspring co-singing and territorial functions (e.g., co-singing more during intergroup encounters or closer to home range borders). Our results suggest that mothers' songs may trigger male offspring and females to practice singing, but not specifically for males to defend territories. We highlight that despite the absence of duets, *H. moloch* develop their vocalizations from early infancy and throughout their maturation while co-singing with mothers. However, the level of co-singing varies depending on the sexes. Our study is the first to elucidate the sex-specific trajectories of vocal development in *H. moloch* across years, indicating that offspring in non-duetting gibbons co-sing with mothers like in duetting species.

KEYWORDS

co-singing, immature, duet acoustics, Javan gibbon, vocal development

Introduction

Humans socially learn speech coordination, vocalization usage, and comprehension early in their development (Bruner, 1975). In contrast, the vocalizations of non-human primates were thought to be primarily innate (Winter et al., 1973; Pistorio et al., 2006; Tomasello, 2010). However, recent studies have revealed highly variable and flexible patterns of immature vocalizations in non-human primates. Those developmental changes in vocalization can be influenced by physical maturation, experience, and social feedback on vocal development (Lemasson et al., 2011; Chow et al., 2015; Gultekin and Hage, 2017; Takahashi et al., 2017; Zhang and Ghazanfar, 2018; Gultekin et al., 2021). Many non-human primates exhibit sex differences in their vocalizing behavior. Those sex differences are call types (gibbons: Geissmann, 2002; indris: Giacoma et al., 2010), acoustic features (baboons: Ey et al., 2007; owl monkeys: Garcia de la Chica et al., 2020; titi monkeys: Clink et al., 2019; tamarins: Masataka, 1987), and vocalization usage such as occurrence rates and contexts (colobus monkeys: Bene and Zuberbueler, 2009; macaques: Bernstein and Ehardt, 1985; spider monkeys: Dubreuil et al., 2015). Moreover, many primates exhibit sex differences in vocal ontogeny of immatures (Green, 1981; Tomaszycki et al., 2001; Pistorio et al., 2006; Ey et al., 2007), which might reflect sex differences in adult vocalizations. For instance, adult indris (*Indri indri*) have a sex-specific song repertoire, and the female and male juveniles differ in their temporal song parameters (De Gregorio et al., 2022). However, little is known about the sex-specific development of primates' vocalization.

Gibbons (Hylobatidae) are excellent models to study the ontogeny and evolution of vocalizations because of their loud and elaborate songs and the phylogenetic position between great apes and monkeys (Raemaekers et al., 1984). Their songs are innate and species- and sex-specific, and these characteristics are inherited (Brockelman and Schilling, 1984). The most remarkable trait of Hylobatidae is duetting in pairs. These duets mainly consist of antiphonal or simultaneous emissions of stereotyped female great calls consisting of a series of notes with increasing tempo and pitch (Marshall and Marshall, 1976), and variable short-notes of males (Geissmann, 2002). However, *Hylobates moloch*, our study subject, is one of the only two non-duetting gibbon species together with Kloss's gibbons (*Hylobates klossii*), and females and males produce only solo songs (Tenaza, 1976; Kappeler, 1984). Lar gibbons (*Hylobates lar*) males and *H. moloch* females in captivity have been recorded to produce highly coordinated duets, the loss of duet in *H. moloch* is likely derived secondarily from duetting characteristics (Geissmann, 2002). Similarly, a loss of duet might be a derived trait from common ancestors (i.e., synapomorphy) shared by *H. moloch* and *H. klossii* (Chan et al., 2010; Roos, 2016; but see Gani et al., 2021). Moreover, *H. moloch* males rarely sing solos as well compared to females regularly sing solos (Kappeler, 1984; Geissmann and Nijman, 2006). Since the pattern of sexual dimorphism in the adult vocalization is different in duetting and non-duetting species, this may influence immature vocal development in non-duetting species differently from those in duetting species. Yet, little is known about the development of vocalization in gibbons.

Immature female gibbons develop their ability to perform great calls (i.e., vocal control and acoustic structures) by co-singing with their mothers, in several gibbon species (*H. lar*; Reichard, 2003, *H. klossii*; Tilson, 1981; Whitten, 1982, *Hylobates agilis;* Koda et al., 2013, and yellow-cheeked gibbons; *Nomascus gabriellae*; Merker and Cox, 1999). Co-singing can indicate the strength of bonding between mother and daughter (Koda et al., 2013; Koda, 2016). Furthermore, gibbon mothers may trigger and tutor their daughters by adjusting their vocal structures according to their daughters' responses (Koda et al., 2013). Immature male gibbons also sing female-specific parts when co-singing with their mothers. This behavior has been reported in duetting gibbons such as *H. lar* and agile gibbons (*H. agilis*; Koda et al., 2014), and *N. gabriellae,* northern white-cheeked gibbon (*Nomascus leucogenys*), and black crested gibbons (*Nomascus concolor*; Schilling, 1984; Hradec et al., 2016, 2017, 2021). With physical and sexual maturation, young males of *N. gabriellae* transitioned from female-like songs to a mix of both male and female-like song parts, to male calls only (Hradec et al., 2021). Similar to immature female gibbons, immature males may also co-sing with their mothers to practice vocalizing.

Adult male *H. moloch* sing solos extremely rare, for example only one single male song was heard during 130 full day survey in West Java (Kappeler, 1984) and male solos were 8.5% of all songs heard in Central Java (Geissmann and Nijman, 2006). However, we observed immature *H. moloch* males co-singing with their mothers' song. Male immatures' co-singing with mothers in non-duetting *H. moloch* may relate to territorial defense like the adult female songs or duets (Mitani, 1985; Geissmann and Orgeldinger, 2000; Fan et al., 2009; Ham et al., 2017). Primate vocalizations, especially duets, are often used to defend their territory by advertising the territorial border or their physical condition (i.e., fighting ability; Mitani, 1987; Barelli et al., 2013). For example, adult female *H. moloch* produced songs more often in the area of their home range that overlapped with neighboring groups than expected based on time spent in the overlapping area versus interior area (Ham et al., 2017; Yi et al., 2020). This suggested that songs of adult female *H. moloch* function for territorial defense by advertising territorial boundaries (Ham et al., 2017), like other primate species (southern brown howler monkeys: da Cunha and Jalles-Filho, 2007; titi monkeys: Robinson, 1979). Thus, *H. moloch* immature males may be triggered to co-sing with their mothers more frequently in similar contexts.

This study aims to understand the development of sexually dimorphic vocalization in Javan gibbons (*H. moloch*). To understand how the vocal ontogeny of *H. moloch* differs between sexes, we investigated vocal development in *H. moloch* offspring in Gunung Halimun-Salak National Park, Indonesia, between 2009 and 2021. First, we tested for sex differences in vocal development in offspring *H. moloch*. Since *H. moloch* adult females produce solo songs more frequently than adult males while there is no duetting, we hypothesized that the differences between adult female and adult male vocalizations should be reflected in co-singing with adult females during vocal ontogeny of offspring as well. We specifically predicted that (1) female offspring will start co-singing with their mothers at an earlier age than male offspring, (2) females will co-sing with their mothers more often than male offspring, and (3) the frequency of co-singing will increase as female offspring get older, in opposition with the co-singing activity of male offspring. Then, we investigated why male offspring *H. moloch* co-sing with their mothers despite the absence of duets and the rarity of adult male solo songs. We hypothesized that male offspring co-singing in *H. moloch* is used for territorial defense similar to that of mothers. Specifically, we predicted that male offspring would co-sing with their mothers more often (1) during intergroup encounters compared to the non-intergroup encounter context and (2) close to their home range border compared to the center of their home ranges. Finally, we reported opportunistically collected cases of adult male and offspring solos.

Methods and materials

Data collection

We have been habituating and following wild *H. moloch* in Citalahab Forest, Gunung Halimun-Salak National Park, West Java, Indonesia (S 6°44′19″E 106°31′45″), as part of a long-term project called the Javan Gibbon Research and Conservation Project (Kim et al., 2012; Ham et al., 2017; Oktaviani et al., 2018; Yi et al., 2020; Jang et al., 2021). We collected data from three habituated gibbon groups and each gibbon group consists of one adult female, one adult male and 2–3 offspring (**Table 1**). During the study period, we observed 13 offspring from the three gibbon groups (male; $N = 9$, female; $N = 4$). They were distributed in four age categories (infant: 0–2 year, juvenile: 2–5 year, adolescent: 5–8 year, subadult: >8 year; definitions following Brockelman et al., 1998). Whenever there were adult female or male vocal events, we recorded the presence of any offspring co-singing and the Global Positioning System (GPS) coordinates. We defined co-singing as two individuals (mother and her immature offspring in our study) vocalizing simultaneously (Koda et al., 2013; Hradec et al., 2021), while duetting is usually defined as coordinated vocalization between a female and male pair in gibbons (Marshall and Marshall, 1976). When an offspring co-sang with an adult, we also recorded the age of the offspring. We calculated the age of offspring from the date of birth. For the individuals without exact birth information ($N_{\text{offspring}} = 5$), we calculated the inter-birth interval of the study population between 2010 and 2021 ($N_{\text{offspring}} = 10$; N within − group inter − birth interval $= 7$; mean ± SD = 1,295 ± 242 days) and subtracted that from the date of birth of the next-born individual with exact birth information in the same group. We compared the body size and behaviors (e.g., spatial distance with other group members) of the individuals with putative age with those of the individuals with known exact age. Then we confirmed no obvious mismatch between the putative age and the body size/behaviors. We also recorded whether co-singing occurred during the intergroup encounters. We excluded the data for which the intergroup encounter context could not be determined for the analyses. We collected GPS coordinates of adult gibbons at 15-min intervals from 2014 to 2019 and 10-min from 2020 to 2021. We followed a gibbon group from a sleeping tree to the next between 0600 and 1700 h.

In addition, we opportunistically observed fourteen cases of offspring vocalization without an adult female vocalization prior. We also recorded 51 male solos from both the focal and the neighboring groups during the study period. Among these, we could confirm the identity of the singers for 41 cases (22 cases

TABLE 1 The life history of the study subjects and data collection period for each gibbon group in Gunung Halimun-Salak National Park, Indonesia between 2009 and 2021.

Group	Data collection period	Individual	Sex	Class	Date of birth	Record
A	Jul 2009–Mar 2010, Mar–Nov 2011, Feb–Jul 2012, Feb–Dec 2013, Dec 2014–Jul 2016, Nov 2016–Aug 2017, Dec 2018–Feb 2021	Aris	Male	Adult	Unknown	
		Ayu	Female	Adult	Unknown	
		Asri	Female	Offspring	Nov 2003*	Dispersed in Aug 2011
		Amran	Female	Offspring	Jun 2007*	Disappeared in Aug 2011
		Amore	Male	Offspring	Dec 2010	
		Awan	Male	Offspring	Dec 2013	
		Ajaib	?	Offspring	Oct 2018	
B	Jul 2009–Mar 2010, Mar–Nov 2011, Feb–Jul 2012, Feb–Dec 2013, Dec 2014–Jul 2016, Nov 2016–Aug 2017, Dec 2018–Feb 2021	Bang Kumis	Male	Adult	Unknown	
		Bu Keti	Female	Adult	Unknown	
		Bayi KumKum	Male	Offspring	Jul 2007	Disappeared in Sep 2007
		Bayi Kimkim	Male	Offspring	Apr 2011	Dispersed in Jan 2020
		Bayi Komeng	Male	Offspring	May 2014	
		Bayi Kendeng	Male	Offspring	Nov 2017	
S	Feb–Dec 2013, Dec 2014–Jul 2016, Nov 2016–Aug 2017, Dec 2018–Feb 2021	Sahri	Male	Adult	Unknown	
		Surti	Female	Adult	Unknown	
		Surono	Male	Offspring	Oct 2003*	Dispersed in Feb 2014
		Sendi	Female	Offspring	Apr 2007*	Dispersed in Apr 2016
		Salwa	Male	Offspring	Nov 2010*	
		Sanha	Female	Offspring	May 2014	
		Setia	Male	Offspring	Jan 2018	

*A star next to the date of birth indicates that it has been calculated from the inter-birth interval of the study population.

from the focal groups and 19 cases from non-focal groups with visual contact).

Data analyses

First, we checked the age at which offspring males and females start co-singing with their mothers. To do so, we investigated the first record of co-singing between offspring and adult females. Additionally, we calculated the mean age of the first *five* co-singing events. We chose five events to overcome the potential observation bias of describing only the first event as we may have missed some co-singing events, for instance, while not following the focal group. Following this protocol, we included sufficient data to calculate mean values ($N_{\text{offspring}} = 5$), while restricting the range of age used to describe the starting age of co-singing. For those with assumed age calculated with inter-birth interval, we did not include them in the calculation in the first or first five co-singing events of co-singing.

To determine the co-singing rates of offspring with mothers, we created a list of female songs ($N_{\text{femalesong}} = 240$) for each offspring individual per day ($N_{\text{total}} = 556$). When adult females stopped singing more than 5 mins before starting to sing again, we defined it as two different song bouts (hereafter "song" Geissmann, 2002). For example, if an offspring co-sang with at least one female song during the day, we marked the day as an offspring co-singing present. For example, if an adult female sang twice a day, and one of the songs was followed by a juvenile but not by an infant of the focal group, we had a line for each immature for that day, one marked with the juvenile co-singing present and the other marked with the infant co-singing absent. Adult females typically sang one song bouts a day and a maximum of up to three bouts. We analyzed our data on a daily base to compensate for the potential of missing data.

We ran a binomial Generalized Linear Mixed Model (GLMM) with the presence of offspring co-singing with the female songs as the response variable ($N_{\text{total}} = 532$), and the offspring age, sex, and the interaction between the offspring age and sex as test predictors, and interaction between the offspring sex and season (dry, semidry, and wet) to control for a potential seasonal effect. We included the gibbon group ID, offspring ID, and each adult female vocalization event ID as random effects. We added the offspring age and season within gibbon group and offspring ID as random slopes.

We estimated the annual home range of each focal group using 95% kernel density estimates (Worton, 1989) to investigate the effect of the location of female vocalizations and the intergroup encounter on the probability of co-singing in offspring males. We calculated the Euclidean distance between the location of female vocalization and the nearest home range border. If a female sang outside the estimated annual home range, we marked the distance to the closest border with a negative value to differentiate the coordinates inside and outside the home range. The distance was divided by the size of the annual home range (ha) to control the potential effect of the home range size difference between groups. We conducted the spatial analyses using ArcGIS Pro (version 2.8.5; Environmental Systems Research Institute, 2022). Then we ran the second binomial GLMM with the presence of offspring males co-singing to the female songs as the response variable. This has been calculated the same way as co-singing rates of offspring with mothers, we created a list of female songs of which the GPS location was identified ($N_{\text{femalesong}} = 110$) for each male offspring individual per day ($N_{\text{total}} = 242$). We included the distance from the home range border divided by the home range size and the context (intergroup encounter/non-intergroup encounter) as test predictors. Then, we included the group ID and offspring ID as random effects, and the two predictors (i.e., the distance from home range border divided by the home range size, and the intergroup encounter context) within gibbon group and offspring ID as random slopes.

Before running the two binomial GLMMs, we visually checked the homogeneity of variance and *z*-transformed all covariates in the models. We also checked for multicollinearity using the R package *car* (Fox and Weisberg, 2019) and did not find a problem since the variance inflation factor (VIF) values ranged between 1.68 and 2.79. We presented the results only when the full-null model comparison was statistically significant, while the null model was only with the random effect and slopes included. All data were analyzed using R (version 4.1.0; R Core Team, 2021).

Results

We recorded 240 female songs, and among these, 95 cases of co-singing between offspring and mothers, and 51 male solos over 82 months of surveys between 2009 and 2021 (**Figure 1**). The age of the first recording of offspring co-singing with their mothers was 23.8 ± 18.8 months (mean ± SD; range: 7.0–60.0; $N_{\text{offspring}} = 8$; **Figure 2**). The age of the first five recordings of offspring co-singing with their mothers was 42.4 ± 16.3 months (mean ± SD; range: 17.2–62.4; $N_{\text{offspring}} = 5$; **Figure 2**). Since we had first recordings of only one female offspring, we could not compare the age of first recordings between sexes directly. Although not included in the study period, we observed a 2-month-old infant (born in November 2021) of unknown sex co-singing with the mother in group A, one of our focal gibbon groups, in February 2022 (**Supplementary Audio 1**). This is the earliest record of infant gibbon co-singing.

In general, the rate of each offspring co-singing with their mothers' songs (i.e., number of female songs that offspring co-sung with/total number of female songs produced) was 0.159 ± 0.153 (mean ± SD; $N_{\text{offspring}} = 13$). Probability of co-singing with mothers changed across developmental stages in both female and male offspring (infancy: 0.091 ± 0.101, juvenility: 0.160 ± 0.141, adolescence: 0.234 ± 0.195, subadult period: 0; **Supplementary Figure 1**).

We found that the interaction between offspring age and sex and between offspring sex and season significantly affected the presence of offspring co-singing with their mother songs (full-null model comparison: $\chi^2 = 6.912$, $df = 2$, $p = 0.032$; **Table 2** and **Supplementary Table 1**). The results indicate that as female offspring become older, the probability of female offspring co-singing with their mothers increased while that of male offspring did not (**Figure 3**). The full model testing the effect of distance from the home range border and the intergroup encounter on co-singing between male offspring and mothers did not fit significantly better than the null model (full-null model comparison: $\chi^2 = 2.059$, $df = 2$, $p = 0.357$).

We found that a female offspring and two male offspring produced vocalizations without the presence of adult vocalization ($N_{\text{vocalization}} = 12$). While female offspring produced vocalizations similar to female great calls even without adult female singing, male offspring produced adult male-like sounds which were not observed when they co-sung with their mothers. The average age of sex-specific vocalization of offspring without adults is 90 months ($N_{\text{offspring}} = 1$) for a female offspring and 98 ± 2.8 (mean ± SD; $N_{\text{offspring}} = 2$) months for male offspring. 75% of these vocalizations were observed during intergroup encounters ($N_{\text{vocalization}} = 9$). All vocalizations of focal subadult males occurred during intergroup encounters ($N_{\text{vocalization}} = 7$). Subadult males from two encountering groups simultaneously vocalized before the other group members arrived at the encounter location and after the other members of the groups left. Male offspring also vocalized when the adult male of the neighboring group produced vocalizations. However, we have not heard any offspring co-singing with their fathers, yet we are not able to confirm whether there was co-singing before we started daily follows at 0600, given that male gibbons produce solos at dawn before 0600 h (Raemaekers and Raemaekers, 1985; Geissmann and Nijman, 2006).

Discussion

To our knowledge, this study is the first to record the vocal developmental trajectories in female and male gibbons, covering the entire immature and mature period of offspring. We found considerable differences in vocal development between female and male offspring in non-duetting *H. moloch*. Both immature female and male *H. moloch* started co-singing with their mothers during infancy, which began around 7 months, and started co-singing more stably during early juvenility. However, surprisingly, we also observed a 2-month-old infant co-singing with its mother outside of our study period. At this point, we are not able to firmly conclude which sex starts co-singing with their mothers at an earlier age, since the sex ratio of our study subject is highly biased toward males for the first recordings (male; $N = 7$, female; $N = 1$). In another pair-living and duetting primate species, *I. indri*, immature females started participating in choruses earlier than immature males, which might be related to the earlier maturation of females than males in this species (De Gregorio et al., 2022). To clarify the sex difference in the emergence of co-singing in gibbons, an intensive investigation of their early infancy for both sexes would be needed.

As infant gibbons grew older, however, they exhibited a clear sex difference in the rate of co-singing with mothers, supporting our prediction. On average, *H. moloch* female

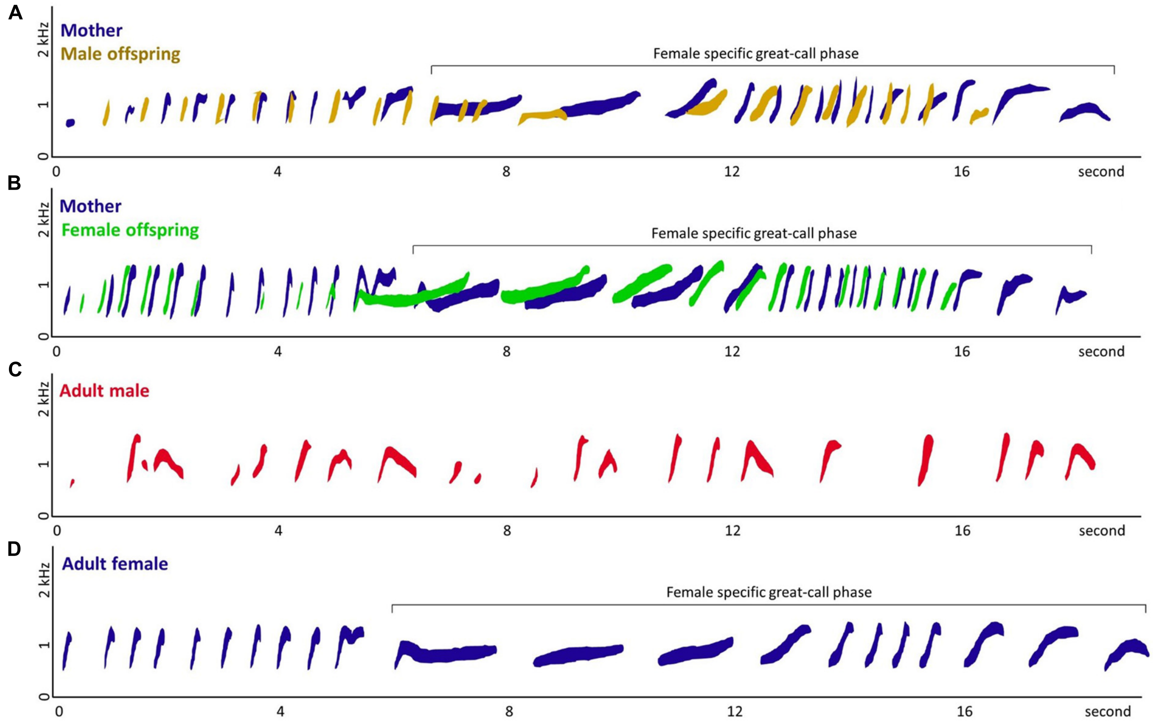

FIGURE 1
Spectrograms of **(A)** co-singing between mother and male offspring, **(B)** co-singing between mother and female offspring, **(C)** adult male solo, and **(D)** adult female solo of *Hylobates moloch*. Panel **(A)** was recorded from gibbon group S, Surti (mother), and Salwa (male offspring; subadult) in September 2019. Panel **(B)** was recorded from gibbon group A, Ayu (mother), and Asri (female offspring; adolescent) in September 2009. Panel **(C)** was recorded from the Javan Gibbon Center, Gunung Gede-Pangrango, Indonesia, in September 2009, due to the difficulty of recording rare adult male solos in the wild. Panel **(D)** was recorded from the gibbon group B, Bu Keti (adult female) in April 2011. Except **(C)** adult male solo, all were recorded from the focal gibbon groups in the study area, Gunung Halimun-Salak National Park, Indonesia. The spectrograms were extracted from the recordings using Raven Lite (Version 2.0.3; Yang, 2022) and we manually traced the spectrograms to specify the callers.

offspring co-sang with their mothers 2.4 times more often than male offspring. Moreover, female offspring co-sang with their mothers more often as they became older. These results support our predictions regarding the difference in vocal development between female and male offspring. This pattern is consistent with *N. gabriellae* females (Merker and Cox, 1999). In contrast, male offspring's engagement in co-singing stayed low throughout development. This sex difference in *H. moloch* seems to be expressed around 2 or 3 years of age, which is still early in their development, given that gibbons wean around 2 years of age (Treesucon, 1984). Co-singing probability with their mothers increased continuously until the female offspring *H. moloch* reached the subadult stage at 8 years of age. From this point on, they were no longer observed co-singing with their mothers, similarly to *H. lar* females (Reichard, 2003). The cessation of co-singing may indicate that female offspring have already acquired adult-level vocalization skills and social independence from mothers (Reichard, 2003; Koda et al., 2013).

In our study, *H. moloch* male offspring also completely stopped co-singing with their mothers at around 7 years of age despite a lower co-singing rate compared to female offspring. In addition, we observed that young males, after 8 years of age, vocalized alone without other group members. Remarkably, while they always produced only female-like great calls when they co-sang with their mothers before 7 years of age, young males produced male-like vocalizations of simple "wa" notes by themselves after 8 years of age. *Nomascus gabriellae* young males also stopped co-singing with their mothers around 7 years old, while gradually switching to adult male songs after producing both female and male type vocalizations between the age of 5–7 years (Hradec et al., 2021). We speculate that these sudden changes in *H. moloch* young male vocalizations might result from hormones related to age and sex, which also may influence the larynx growth and acoustic structures (Newman et al., 2000; Barelli et al., 2013). Further studies should investigate the ontogeny of vocalization with detailed acoustic analyses together with hormonal analyses.

We did not find any relationship between male offspring co-singing with their mothers and territorial defense. Unlike what we predicted, male offspring did not co-sing with their mothers more often during intergroup encounters compared

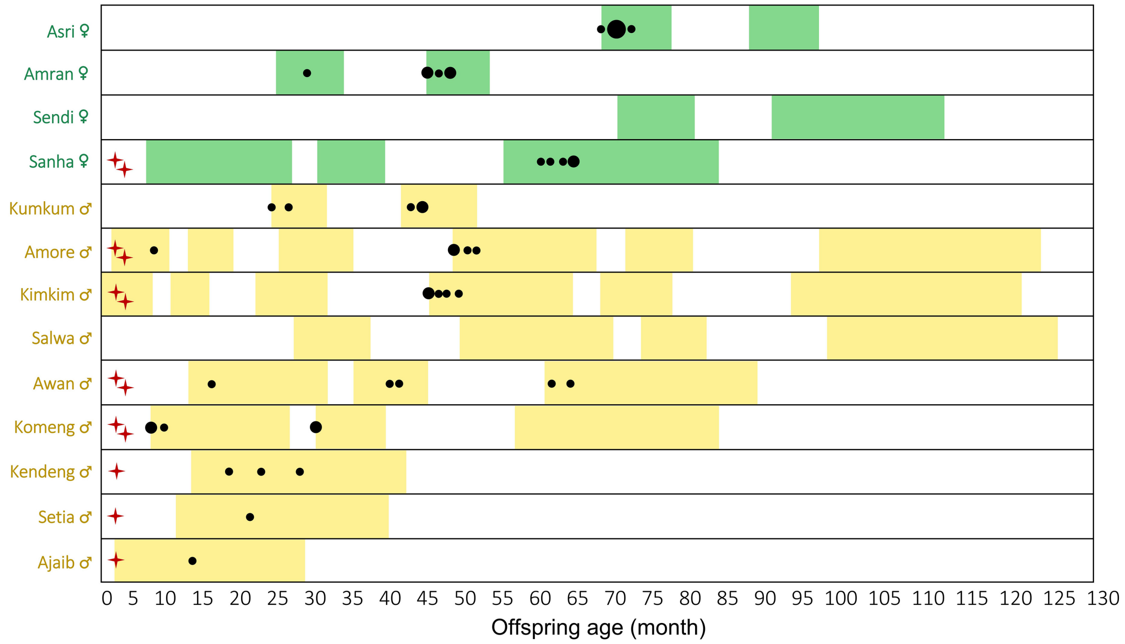

FIGURE 2

The age of the earliest (maximum) five recordings of each offspring *Hylobates moloch* co-singing with mothers in Gunung Halimun-Salak National Park, Indonesia, between 2009 and 2011. The colored bar indicates the data collection period covered in this study. The circle size represents the number of co-singing events (1–3 cases). Red crosses close to the individual name indicate that we included the individuals ($N_{\text{offspring}}$ = 8) in calculating the age of the first co-singing record, and two crosses indicate that we included the individuals ($N_{\text{offspring}}$ = 5) in calculating the age of the first five co-singing records. Individuals without crosses were not included in the first co-singing records because our study period does not cover their early infancy and likely missed the first records.

to the non-intergroup encounter context, or close to their home range border compared to the center. During the study period, we recorded only six cases of vocalizations produced in intergroup encounters from the focal adult males over the 82 months of the study period (e.g., 132 female songs produced in intergroup encounters in the same period). Considering *H. moloch* adult females defend territories by singing solos at the overlapping area with neighbors and advertising the

TABLE 2 The result of the binomial Generalized Linear Mixed Model (GLMM) investigating the effect of offspring age, sex, and season on the offspring *Hylobates moloch* co-singing with their mothers in Gunung Halimun-Salak National Park, Indonesia from 2009 to 2021.

	Estimate	Std. error	*z*-Value	*P*-Value
Offspring age[1]	1.484	0.560	2.648	0.008**
Offspring sex (male)[2]	1.785	1.412	1.265	0.206
Offspring age × sex (male)	−1.642	0.541	−3.035	0.002**
Season (semidry)[2]	4.290	1.560	2.750	0.006**
Season (dry)[2]	3.989	1.548	2.577	0.010**
Offspring sex (male) × Season (semidry)	−3.971	1.690	−2.350	0.018*
Offspring sex (male) × Season (dry)	−4.189	1.697	−2.469	0.014*

[1] *z*-transformed (original mean ± SD = 49.52 ± 31.02).

[2] Reference level for offspring sex: female, season: wet.

The significance levels are * < 0.05 and ** < 0.01.

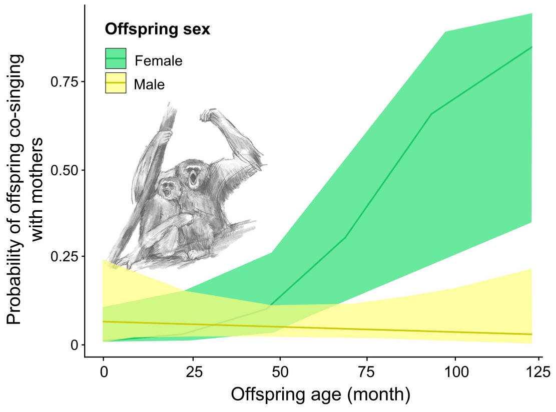

FIGURE 3

The probability of offspring *Hylobates moloch* co-singing with their mothers throughout the ages in Gunung Halimun-Salak National Park, Indonesia, between 2009 and 2021.

borders (Ham et al., 2017), our finding implies that *H. moloch* adult males rarely produce solos for the same purpose of female's territorial defense. However, since *H. moloch* adult males participate in intergroup encounters mostly by chasing (Yi et al., 2020), we speculate that male offspring also do not relate vocalization or co-singing with adult females for territorial defense.

Then what could be the evolutionary function of co-singing in *H. moloch* male offspring? Male offspring may co-sing with their mothers to avoid competition with fathers by producing female-like great calls, and thus by relaying information about their immature status (Hradec et al., 2021). However, this is unlikely because in both *N. gabriellae* (Hradec et al., 2021) and *H. moloch* (present study), co-singing episodes between young males and mothers were no longer observed after 8 years of age. The competition with fathers should peak around the subadult stage (i.e., >8 year). As Geissmann (2002) suggested, the duetting behavior of *H. moloch* and *H. klossii* was likely lost secondarily. We speculate that in duetting ancestors, *H. moloch* male offspring co-singing with their mothers once had the evolutionarily benefit of facilitating the improvement of their vocalization. However, despite the lower benefits of co-singing compared to duetting ancestors, *H. moloch* male offspring might benefit from practicing to achieve varieties of adult male songs and strengthen their bonds with their mothers through co-singing.

Finally, we found that *H. moloch* males rarely but still considerably produced solo songs after 0630 h. We assume that *H. moloch* males vocalize more often than we report here from our opportunistic data, since male gibbons produce solos at dawn (Raemaekers and Raemaekers, 1985; Geissmann and Nijman, 2006). While previous studies mainly focused on the pre-dawn male chorus, there is no detailed description of post-dawn male songs. Despite their rarity, we found that male vocalizations occurred throughout a day between 0630 and 1700 h, and some male vocalizations lasted more than 40 min. Further studies on adult male vocalization will shed light on the evolution of young male vocalization in *H. moloch*.

Our study has limitations in several aspects. First, because of data collection methods (i.e., following one focal group a day), we could have missed co-singing between adults and offspring and offspring solos, even though we tried to overcome this limitation by counting the first five co-singing records. Also, we lack observations in the early dawn, in which adult males might produce solos more. Second, we do not know the exact ages of some offspring born before our research period. Even though we relied on the individuals with exact birth records in the first co-singing events and considered body size and behaviors as other proxies, there may be a slight difference from their actual age. Moreover, we have the biased sex ratio in the focal groups resulting in a small sample size for female offspring. Lastly, we could not compare vocal structures between female and male offspring to examine the similarity with their mothers since we did not have good quality recordings. Instead, we focus more on their behavioral ecology than detailed acoustic analyses. We recommend that future studies investigate the ontogeny of vocal structures in both female and male offspring.

Vocalizations of non-human primates have received great attention due to their phylogenetic closeness to humans. However, there is a dearth of data on the vocal development of non-human primates, probably because of prolonged immature periods, long lifespan, and different methodologies and parameters for various vocal patterns (Harvey and Clutton-Brock, 1985; van Schaik and Isler, 2012). Despite the limitations of our study, our results highlight that *H. moloch* develop their vocalization from early infancy throughout their development while interacting with their mothers. Given their elaborated song structures, co-singing with their mother would help young female *H. moloch* acquire adult-level communication skills. Even though young males co-sing with their mothers less, still, co-singing can help achieve a variety of adult male songs despite potentially lower benefits than their duetting ancestors. Our findings contribute to understanding the non-duetting gibbon's vocal development and emphasize further interdisciplinary and longitudinal studies encompassing social systems, life history, behaviors, and physiology.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Indonesian Ministry of Research and Technology (RISTEK), the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA), and the Gunung Halimun-Salak National Park.

Author contributions

YY and AC conceptualized the initial idea and drafted the manuscript and performed and interpreted the statistical analyses. YY, AC, SL, SH, RO, and HJ collected the behavioral data. YY, AC, SL, SH, RO, HJ, AM, and JC revised, contributed to the article, and confirmed the final version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.910260/full#supplementary-material

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