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Life History and Reproductive Strategies of Khao Yai *Hylobates lar*: Implications for Social Evolution in Apes

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Abstract Among primates, great apes have the most extended life histories and they also appear socially specialized because of their flexible association patterns and sociosexual relationships. Researchers have hypothesized that such subtle social commonalities in combination with a slow life pace lead to great apes advanced cognition. Small apes, in contrast to great apes, are commonly believed to be socially inflexible, and little comparative life history data exist for wild populations. We investigated how the small white-handed gibbon (*Hylobates lar*) fits into a great ape life history and sociality framework. We followed the life histories of adults in 12 groups over *ca.* 18 yr at Khao Yai National Park, Thailand. Results demonstrate that the life histories of white-handed gibbons closely resembled those of other apes. Mean female age at first reproduction was late (11.06 yr), and mean interbirth interval (41±9.1 mo) and juvenile period (9.5±1.8 yr) were long. Multimale grouping of 2 adult males and 1 female was a common alternative (21.2% groups) to the traditional hylobatid pair-living social organization in our population. Female sexual partnerships include a variety of polyandrous mating strategies for both pair-living females and females in multimale groups. From our long-term study a picture of social complexity materializes that resembles social complexities in other apes. In conclusion, we infer that gibbons share commonalities postulated to unite great apes based on similar life histories and very flexible social and sexual relationships.

Keywords age at first reproduction · interbirth interval · mating behavior · polyandry · white-handed gibbon

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Introduction

To understand primate female reproductive strategies comprehensively, long-term demographic data that capture life cycle information are indispensable because life history, ecology, and behavior interact in intimate ways that can effectively constrain sexual strategies (Kappeler *et al*. 2003; Schuster and Wade 2003). In addition, reproductive characteristics may affect individual reproductive success and reproductive potential (Borries *et al*. 2001; Nishida *et al*. 2003).

Researchers have long recognized that primates mature slowly compared to other mammals (Charnov and Berrigan 1993; Harvey *et al*. 1987; Ross 1988; Ross and Jones 1999). More specifically, the great apes are characterized by lengthy growth and a late start of reproduction, which perhaps allows for a particularly extended juvenile period during which important brain development occurs (Deaner *et al*. 2003), and results in the longest birth intervals of any primate including contemporary human hunter-gatherers (Galdikas and Wood 1990; Kaplan *et al*. 2000; Knott 2001; Wich *et al*. 2004). With regard to social life, great apes also appear to be specialized. For example, van Schaik *et al.* (2004) remark that great ape social groups are complex because in great apes: 1) association patterns are more variable; 2) formal dominance is largely absent despite a potential for clear-cut contest competition; 3) strong bonding occurs between nonrelatives; and 4) intraspecific variation in social organization and affiliation is remarkably diverse. All of the traits may ultimately have links to a great ape specific life history that coincides with their large brains (*cf.* van Schaik *et al.* 2004). Beyond the profound variation in social organization, great ape females show a tendency for independent foraging, i.e., they are not constantly in proximity to other females when foraging (Knott and Kahlenberg 2007; Stumpf 2007; Watts 2001), and in African apes and orangutans females commonly disperse or transfer (Boesch and Boesch-Achermann 2000; Stumpf 2007), a trait gibbons share with other apes (Carpenter 1940; Lappan 2007a). Hence, several lines of evidence suggest a flexible social setting for great apes, and great ape females appear to enjoy a variety of options to maximize reproduction, which in itself may have become a distinct great ape trait. However, it is less clear when in hominoid evolution a trend toward a changing life pace and more flexible female reproductive strategies emerged, and further whether or not the small apes and their ancestors already shared such flexibility with the other apes.

In contrast to great apes, gibbons are rarely thought of as socially flexible. Despite growing indications of deviations from a rigidly pair-living social organization and monogamous mating system (Barelli *et al.* 2007, 2008a; Fuentes 2000; Lappan 2007b; Palombit 1994; Reichard 1995, 2003, in press; Savini *et al.* 2008; Sommer and Reichard 2000), researchers still often consider gibbons as behaviorally inflexible and somewhat trapped into a narrow system of segregated pairs (but see Bartlett 2007; Fuentes 2000). Such a perspective, together with a small body (Smith and Jungers 1997) and absolute brain size (Rilling and Seligmann 2002) has resulted in often setting them apart behaviorally and cognitively from the more derived great apes and humans (Gebo 2004; Povinelli and Cant 1995).

However, owing to the limited number of long-term studies on hylobatids, few life history data are available for wild gibbons vs. the wealth of knowledge from long-term studies of chimpanzees, mountain gorillas, and orangutans. Bartlett's (2007) comprehensive gibbon review summarizing advances of the past 2 decades only provides *ca.* 7 mo for gestation length (Carpenter 1940; Geissmann 1991; Leighton 1987), and an age at first reproduction for captive females between 6 and 9 yr (Geissmann 1991) and *ca.* 8–10 yr for wild gibbons (Carpenter 1940). Moreover, wild gibbon females have been noticed to reproduce at long intervals of 10 yr (Chivers and Raemaekers 1980) or as short as ≤2 yr or only 1.8 yr (Ellefson 1974; Palombit 1995), though most reports from wild populations hover at *ca.* 3–4 yr (Bartlett 2007; Chivers and Raemaekers 1980; Mitani 1990; Palombit 1995).

In the context of amassing comparative primate life history data to understand better the evolution of the unique human life history (Kaplan *et al.* 2000), studying gibbons is particularly rewarding because with a body mass <10 kg (Smith and Jungers 1997; except for the larger siamang, *Symphalangus syndactylus*) gibbons resemble medium-sized monkeys more than they resemble great apes though ancestral hylobatids were probably larger (*cf.* Begun 2004; Gebo 2004). Lee (1999), Lee *et al.* (1991) and Ross and Jones (1999) argued that body mass importantly influences the pace of life, with larger species generally showing slower life cycles than smaller species. Thus, based on body mass alone, gibbons should have life cycles that resemble those of monkeys more than those of great apes. Alternatively, their recent divergence from the hominoid lineage (Chatterjee 2006; Hacia 2001; Raaum *et al.* 2005; Roos and Geissmann 2001) and secondary size reduction (Begun 2004) may advocate for stronger similarities with great apes. Anatomical traits such as the well known Y-5 lower molar pattern, the absence of a tail, and unique upper body and forelimb adaptations clearly identify gibbons as apes, which is also reflected in a partially enlarged brain vs. that of monkeys (MacLeod 2004; Rilling and Insel 1998, 1999; Schenker *et al.* 2005). Brain size is another trait that correlates with the speed of life (Deaner *et al.* 2003; Ross 2004; Ross and Jones 1999; van Schaik and Deaner 2003), which further predicts that gibbon life histories are most similar to those of other apes, though brain size also correlates positively with body mass (Deacon 1997; Ward *et al.* 2004).

We aimed to provide new data from the Khao Yai long-term behavioral ecology project to place one of the smallest gibbon species —the white-handed gibbon (*Hylobates lar*)— into a framework of life history patterns and reproductive strategies of monkeys of similar body mass and great apes. We realized that it would have been difficult to prioritize *a priori* testing body mass over phylogeny with regard to the gibbon life history, because both variables influence it (Kappeler and Pereira 2003; Lee 1999). We decided to test the null hypothesis that basic life history variables resemble those in similar-sized monkeys 1) because of the important influence of body mass on life cycles (Ross and Jones 1999), 2) because we have access to data allowing us to compare body size to life history, and 3) because researchers have hypothesized large body size as an eminent precondition for the evolution of slow life histories in great apes (van Schaik *et al.* 2004). Based on the prediction of similarity in life history between monkeys and gibbons, we further hypothesize that gibbon female reproductive strategies would also differ significantly from those of other ape females.

To grasp female reproductive strategies we provide data on the variation of group size and composition in addition to data on mating behavior from an ongoing gibbon field study. We compare the data to those of other apes and selected monkeys to identify overlap and disparity of variables and to show how one can interpret the evolutionary position of white-handed gibbons.

Methods

Study Site

Khao Yai National Park (KY) is a tropical seasonal rain forest (Kitamura *et al.* 2005). The park was established in 1962, covers *ca.* 2168 km^2 (101°22′E, 14°26′N) of continuous forest, and is part of the large Dong Phayayen–Khao Yai (DPKY) World Heritage forest complex (6199 km^2; UNESCO 2005). KY ranges at an elevation of *ca.* 100–1300 m and rainfall varies from 2000 to 4900 mm annually (Kitamura *et al.* 2004; Savini *et al.* 2008). Most precipitation occurs during a 6-mo wet season (May–October), whereas November–April are usually dry. Annual diurnal temperature varies between 18.7 and 28.3°C, with the lowest temperatures usually occurring in December and January, e.g. 1999–2003 mean temperature: 16.3/15.8°C respectively; range: 7–21° C. Humidity at the site ranges from an average 64.6% during the dry season to 77.1% in the wet season.

We conducted the study at the Mo Singto–Klong E-Tau research site in the central portion of KY (Reichard in press), where the population density is 15.9 individuals/km^2 (Barelli *et al.* 2007).

Subjects

White-handed gibbons are sexually monomorphic, reach a body mass of 5–6 kg (Smith and Jungers 1997) and females give birth to single offspring. Individual members of 1 study group were habituated to the presence of observers in 1989, and by 1999 members of all groups were habituated. Overall, we include demographic and behavioral data of 17 females and their 24 male partners. Individual data contributions varied notably owing to habituation status, observation schedules, and the time adult individuals spent in the research site. Individual ages were well known for individuals born after 1989.

Time of Data Collection and Behavioral Observations

We collected data from members of 12 groups between October 1989 and September 2007 (18 yr) and annual census data are available from 1992 to 2007, except 1995, when we conducted no census (we added 1 birth occurring in June 2008 to the sample). Census data reflect group compositions during the last quarter of the calendar year (October–December) except in 2007, when we conducted a census in September. For 7 groups, monitoring started in 1992, whereas we successively added the remaining 5 groups to the sample as they formed or became habituated during the study (groups: R, 1993; D, 1996; J, 1998; T, 1998; W, 1999). Details of group histories are available elsewhere (Brockelman *et al.* 1998; Savini *et al.* submitted). Overall, of the 12 groups, 5 groups contributed census data over 15 yr, 2 groups over 13 yr, 2 groups over 10 yr, and the 3 remaining groups over 14, 12, and 9 yr, respectively. Thirty-one observers and volunteers contributed information to the white-handed gibbon long-term project during the period we report here (see also Savini *et al.* 2008).

Analyses summarize records *ad libitum* and systematic focal individual ones (Martin and Bateson 1993) during >3000 contact hours. Because of the time depths and large sample, observation of individuals ranged from sporadic to systematic daily follows. Despite great individual variation of source data, only precisely known events, i.e., ones accurately dated to ≤1 mo such as births, group composition changes, and deaths/disappearances as well as other life history events entered our analyses.

Birth Seasonality

Per Lindburg (1987, p. 167), we defined reproductive seasonality as “any tendency toward temporal clustering of reproductive activity, either discrete seasons or seasonal peaks.” Accordingly, a birth season is “a discrete period of the year to which all births are confined. There must be some months in which no births occur” (Lancaster and Lee 1965, p. 488), whereas a birth peak is “the period of the year in which a high proportion of births but not all birth are concentrated” (Lancaster and Lee 1965, p. 488). For an analysis of birth seasonality, we exclusively considered births for which we were certain parturition had occurred in a ≤2-wk time window (parturition date ±1 wk) and could place the birth precisely within the limits of a given month.

Statistical Analyses

We provide standard deviation of means if not indicated otherwise. To establish whether a seasonal pattern in reproduction existed we used Rayleigh’s test (R Development Core Team 2006; Zar 1999) with circular release 0.3–6 (Lund and Agostinelli 2006), which indicated whether the months when the majority of births clustered differed significantly from the rest of the year. To describe group composition variation, we provide descriptive statistics as averages across the entire, large data set for clarity. All tests are 2-tailed with an α error=0.05. We conducted statistical testing on SPSS release 14.0.

Results

Group Size and Composition

Changes in group composition occur due to birth, immigration, emigration, and death/disappearance. Study groups range from 2 to 6 individuals (mean=4.2±0.9 individuals), with a mean adult group size of 2.5 individuals (N=156 census groups). There is a mean of 1.1 adult females and 1.5 adult males (including mature male offspring) per group, yielding an overall male biased sex ratio of 1.4 males per 1 female. Across census years the average proportion of pairs is 76.9% (N=120), whereas multimale single-female groups accounted for 21.2% (N=33; groups with mature male offspring excluded) on average and single-male multifemale groups for 1.9% of social units (Table I).

Age at First Reproduction

Of 14 females that reached adulthood during the study, only 4 remained in the site and gave birth for the first time at a mean age of 11.06 yr. We knew Hima’s birth to

Table I Group structure frequencies of twelve habituated white-handed gibbon groups, Khao Yai National Park, Thailand

Census#	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	mean ± SD
Pairs [n]	6	7	6	–	7	8	9	10	9	10	9	7	7	8	8	9	
[%]	85.7	87.5	85.7	–	77.8	88.9	81.8	83.3	75.0	83.3	75.0	70.0	63.6	66.7	66.7	75.0	76.9±8.2
Multimale groups [n]	1	1	1	–	2	1	1	1	2	2	3	3	4	4	4	3	
[%]	14.3	12.5	14.3	–	22.2	11.1	9.1	8.3	16.7	16.7	17.2	23.1	33.3	33.3	33.3	25.0	21.2±8.7
Multifemale groups [n]	0	0	0	–	0	0	1	1	1	0	0	0	0	0	0	0	
[%]	0	0	0	–	0	0	9.1	8.3	8.3	0.0	0	0	0	0	0	0	1.9±3.6
Total	7	8	7	–	9	9	11	12	12	12	12	10	11	12	12	12	

data collected during last quarter of calendar year (October - December) except for 2007 when census data were collected in September.
"–" no census conducted.

within ±2 mo and recorded her first parturition within ±3 d, revealing an age at first reproduction of 10.9±0.1 yr. Considering a 7-mo gestation period, Hima's first conception occurred at the age of 10.25±0.1 yr. We knew Rung's birth date to within ±2 d and recorded her first parturition within ±1 wk, resulting in an age at first reproduction of 10.7 yr and an estimated age at first conception of 10.17 yr. We knew female Jojo's birth date to within ±1 mo and we recorded her first parturition within ±10 d, revealing an age at first reproduction of 10.0 yr and an estimated age at first conception of 9.42 yr.We knew the birth date of a fourth female, Brenda, less well because she was a *ca.* 3.5±0.5 yr-old juvenile when we first recognized her in a study group. We calculated her age at first reproduction as 12.5±0.5 yr. However, Brenda's estimated age at first reproduction was slightly more complex because we suspected that she had lost a fetus in the year before her first parturition. In that year, when she was 11.6±0.5 yr old, she displayed conspicuous abdominal distension characteristic of the final 1–2 mo of gestation (*cf.* Kawakami and Kollias 1984; Palombit 1995). We noticed abrupt reduction in abdominal distention shortly after an intense intergroup encounter, i.e., an encounter with multiple close-range chases. Later that day, we noticed traces of blood around Brenda's genital area and on the following days her abdominal distention had disappeared, suggesting premature pregnancy termination. A 2-d search for the fetus was unsuccessful. Considering that Brenda was pregnant and close to parturition when she lost her first infant reveals an estimated age at first conception of *ca.* 11.17±0.6 yr.

Though it is yet unknown at which age wild gibbon females reach menarche, and whether or not they experience a period of sterility before first conception, a recent hormone based study of female ovarian activities (Barelli *et al.* 2007) indicated first elongated vulval tumescence with a conspicuous mass of pink tissue (*cf.* sexual swelling) for Hima at *ca.* 8.25 yr and for Rung at *ca.* 8.08 yr of age, while both females still resided in their respective natal groups. However, neither female showed a cyclical pattern of progestogen levels that would have allowed distinguishing a follicular from a luteal phase and we detected no menarche before their natal dispersals (Barelli *et al.* 2007). Accordingly, it seems likely that both females at *ca.* 8 yr had not yet attained reproductive capacity. However, after natal dispersals and settling into new groups, they conceived quickly (Hima: 1.08 yr after natal dispersal; Rung: 5–9 mo after natal dispersal; backdated from emigration and first parturition).

Interbirth Intervals

During the study, we recorded 17 complete interbirth intervals with precise parturition estimates for 9 females. Mean birth interval is 41±9.1 mo or 3.42±0.76 yr (range=34–71 mo; N=17). When an infant died before completion of weaning, female interbirth intervals were significantly shorter (mean=25±9.0 mo or 2.01±0.75 yr; range=11–37 mo; N=7; independent sample t-test: $t_{22}=3.896$, $p<0.01$), which remained significant also when we compared individual female interbirth intervals (paired-samples t-test: $t_5=2.68$, $p<0.04$).

Overall, we recorded a total of 46 births in study groups between October 1989 and September 2007 and for 24 infants we know the birth month with certainty. We recorded births in every calendar month of the year except May and December, indicating that Khao Yai females can potentially give birth year-round. Nevertheless, the distribution of births showed a peak (Rayleigh test: $R=0.4988$; $N=24$; $p=0.0019$) with highest birth frequencies in September ($N=5$) and October ($N=7$), around the tail end of the rainy season and the beginning dry season, when 70.8% of the births occurred.

Infant and Juvenile Survival

Of 44 infants born in the population (we excluded 2 infants from analysis because they were <1 yr old in September 2007), only 3 died before reaching 1 yr of age revealing a low infant mortality in the first year of 6.3%. Of infants surviving the first year, 86.5% survived through weaning ($N=37$); 89.3% of which reached 5 yr ($N=28$), and thereafter 85% achieved maturity ($N=20$). Of 17 individuals that reached dispersal age, 9 had dispersed successfully because they either were seen in other groups or ≥1 home range away from their natal range. Five individuals dispersed/disappeared from the natal group with unknown fate, and 3 males delayed dispersal at 8.5 yr, 9.8 yr, and 14.9 yr, respectively, when data collection ended.

Length of Juvenile Period

We calculated an average length of the juvenile period, defined as the time at first reproduction minus infancy, for Khao Yai white-handed gibbons of 9.5±1.8 yr based on our data of female age at first reproduction and Treesucon's (1984) data of weaning age of 2 infants from the study population (weaning ages were 21 and 23 mo, respectively). However, given the very small sample for age at weaning, one must treat the data with caution even though our qualitative long-term demographic records support a mean weaning age of *ca.* 2 yr.

Female Social and Sexual Partnerships

We recorded 26 adult females in the focal population between January 1992 and September 2007 (Table II). Because we aimed to capture female long-term social and mating strategies, we divided the sample by female residence. We considered adult females that stayed ≥3 years in the study population as long-term residents ($N=11$) and otherwise short-term residents ($N=15$). Though for most short-term resident females neither social nor sexual partnerships occurred, we maintained the data to highlight the importance of long-term observations and because a few short-term resident females' mating patterns appeared to be as flexible as those of most long-term resident females.

Of all females, 12 inhabitants were adult at the onset of behavioral observations, whereas 14 reached adulthood during the study. Of females that reached adulthood, 7 disappeared after natal dispersal and 2 stayed only briefly before they likewise disappeared/dispersed. Only 5 matured females developed recognizable social partnerships within the study community, i.e., they duetted, allogroomed, and continuously traveled with 1 or more male partners. One of them dispersed from her natal group into a neighboring group, replacing the resident female and forming a multimale group with the 2 related resident males. Owing to the time depth of our study, most long-term resident females experienced periods of pair-living as well as multimale groups at various times. In contrast, recorded social partnerships for short-term residents were either pair-living (*N*=4) or multimale groups (*N*=2), suggesting that we likely did not record the full breath of social partnerships for short-term resident females.

The mating partnerships of females were likewise flexible. Female monandry was rare and seen only in short-term resident females (*N*=3). All sexually active long-term resident females and half of the short-term resident females were sexually polyandrous (*N*=11), i.e., they maintained simultaneous sexual relationships with ≥2 males (Table II). Female sexual polyandry was complex and expanded beyond social partnerships. Pair-living females copulated with their current and previous social partner(s) and neighboring males with whom they had no close sociospatial relationship: extrapair copulations (EPCs). All females living in multimale groups copulated with both males in the group and some females also had EPCs with neighboring males. Seven of 11 (64%) long-term and 1 of 15 (7%) short-term resident females were observed to engage in EPCs.

Discussion

We aimed to provide basic life history and female reproductive strategy data of a large, wild white-handed gibbon population and to develop a coherent framework to interpret the gibbon life history. Based on our data and analyses, we reject the hypothesis of similarity between gibbons and same-sized monkeys. Instead, great resemblance occurs with great apes.

In the following, we discuss how our results compare to those of other gibbon studies, same-sized monkeys, i.e., primate species with females of mass 5–6 kg (*cf.* Smith and Jungers 1997), and great apes. We then discuss why gibbons may have slow life histories, integrating life history with female reproductive strategies. Our discussion of gibbon life history is structured in reverse temporal order, i.e., from female age at first reproduction to gestation length.

Female Age at First Reproduction

Though differences in absolute body mass usually explain variation of female age at first reproduction (Ross and Jones 1999), body mass fails to account for a late onset of reproductive careers of Khao Yai white-handed gibbon females. In absolute terms, Khao Yai female mean age at first reproduction is most similar to that of Karisoke mountain gorilla females, and only slightly younger than that of other great ape females. But gibbon females are twice as old and older at the onset of reproduction than similar-sized monkey females (Table III). Though our sample for female age at first reproduction is small, we are confident that the data accurately reflect the typical pattern for Khao Yai females, i.e., an onset of reproduction ≥10 yr, for 2 reasons. First, little variation of age at first reproduction occurred among 4 focal females and none was <10 yr (range 10.0–12.5 yr). The cohesiveness of our data set even increases if we consider female age at first conception. Accepting Brenda's miscarriage reveals a mean female age at first conception of *ca.* 10.25 yr. Second, our long-term demographic records (data not given) indicate that female dispersal commonly occurs between 8 and 10 yr (Brockelman *et al.* 1998), and there is no record of a predispersal female having reproduced, supporting our view that first

Table II Social and sexual partnerships of white-handed gibbon females, 1992 - 2007, Khao Yai National Park, Thailand

	Female		Social partners				Sexual partners			
	Adult at study onset	Reached adulthood during study		1 partner (pair-living)	2 partners (multimale)	>2 partners (multimale)		1 partner (monandrous)	2 partners (polyandrous)	>2 partners (polyandrous)
Short-term residents[a]		Akira[1]	(–)					✓		
		Caleb[1]	(–)					✓		
		Cyrana	(–)						✓	
		Dara	(–)				(–)			
		Hima				✓			✓	
	Jaa[2]			✓			(–)			
		Jojo[3]		✓				✓		
	Mai[2]			✓			(–)			
		Mali	(–)				(–)			
	Marilyn[2]			✓			(–)			
		Naam	(–)							
		Rung*				✓[4]				✓
		Shanti	(–)				(–)			
		Sengfa	(–)				(–)			
		Waraporn	(–)				(–)			
Total:	3	12	9	4	0	2	8	3	2	1

Long-term residents[b]	Andromeda*			✓	✓	✓				✓
	Bridget*			✓						✓
		Brenda*		✓	✓					✓
		Brit*		✓	✓					✓
	Cassandra*			✓		✓[4]				✓
	Daow				✓				✓	
	Hannah			✓			(–)			
	Jenna*				✓				✓	
	Sofi			✓			(–)			
	Natasha				✓[4]		(–)			
	Wolga*			✓					✓	
Total:	9	2	0	8	6	2	3	0	3	5
Grand Total:		26	9	12	6	4	11	3	5	6

Partnerships with ≥2 males are simultaneous unless stated otherwise.
bold = remains resident after natal dispersal.
(–) not observed
✓ observed
[a] resident adult <3 years.
[b] resident adult ≥3 years.
*extra-pair copulations (EPCs) observed.
[1] first seen copulating in natal group; dispersed/disappeared shortly thereafter.
[2] immigrant female.
[3] matured and remained in natal group; socio-sexual partnership with immigrant male.
[4] serial partners.

Table III Basic life history parameters of selected monkeys, Khao Yai white-handed gibbons, and great ape populations

Species	Site	Female body mass [kg]	Age at first reproduction; mean (range) [years]	Interbirth interval; mean [years]	Infant mortality (1st year) [%]	Gestation length; mean [days]	Age at weaning; mean[a] [days]	Juvenile period[b] [years]
Macaca mulatta	-	5.37^{1}	3.00^{2}	1.00^{2}	-	165^{2}	293^{2}	3.05^{2}
Macaca nemestrina	-	$4.9/\ 5.57/\ 6.50^{2}$	3.92^{2}	1.16^{2}	-	169^{2}	300^{2}	2.46^{2}
Macaca nigra	-	$4.60/5.47^{2}$	5.44^{2}	1.50^{2}	-	170^{2}	-	-
Macaca silenus	-	5.00^{2}	4.92^{2}	1.41^{2}	-	181^{2}	365^{2}	3.41^{2}
Cercocebus galeritus	-	5.26^{1}	6.50^{2}	1.41^{9}	-	171^{2}	-	-
Cercocebus torquatus	-	5.50^{1}	4.67^{2}	1.07^{11}	-	171^{2}	-	-
Trachypithecus cristata	-	5.76^{1}	4.00^{2}	1.50^{11}	-	-	365^{2}	-
Hylobates lar	Khao Yai	$5.34/\ 5.46^{1}$	$11.06\ (10\text{-}12)^{6}$	3.42^{6}	6.3^{6}	190^{12}	690^{14}	9.5^{6}
Pongo abelii	Ketambe	35.7^{1}	$15.40\ (13\text{-}18)^{7}$	9.30^{4}	8.0^{4}	-	-	-
	Suaq Balimbing	-	-	8.20^{4}	-	-	-	-
Pongo pygmaeus	Gunung Palung	-	-	7.00^{4}	-	*Pongo pygmaeus* $244/250^{2}$	*Pongo pygmaeus* 1274^{2}	*Pongo pygmaeus* 7.9^{2}
	Tanjung Puting	-	$15.70\ (15\text{-}16)^{7}$	7.70^{4}	-			
Gorilla gorilla beringei	Karisoke	-	10.1 (median) $(8.7\text{-}12.8)^{7}$	3.90 $(\text{median})^{4}$	26.2^{4}	*Gorilla gorilla* $260/285^{2}$	*Gorilla gorilla* 1060^{2}	6.5^{13}
Gorilla gorilla graueri	Kahuzi Biega	-	-	4.60^{4}	19.6^{4}			*Gorilla gorilla* 6.6^{2}
Gorilla gorilla gorilla	Lossi	-	-	-	8.3^{8}			
	Mbeli Bai	-	-	5.19^{8}	$42.9/\ 28.6^{8}$			
Pan troglodytes	Bossou	-	$13.00\ (12\text{-}14)^{7}$	5.10^{4}	-	-	*Pan* ***troglodytes*** $1680/\ 1702/\ 1825^{2}$	-
	Gombe	31.3^{3}	$13.30\ (11.1\text{-}17.2)^{7}$	5.50^{4}	-	228^{16}		8.0^{13}
	Kanyawara	36.9^{4}	$15.40\ (14\text{-}18)^{7}$	6.20^{4}	-	-		*Pan troglodytes* 8.4^{2}
	Mahale	35.2^{5}	13.20 median $(12\text{-}23)^{10}$	5.6 $(\text{median})^{10}$	28.0^{4}	228^{16}		
	Taï	40.4^{1}	$14.30\ (12.5\text{-}18.5)^{15}$	5.80^{15}	30.0^{15}	240^{13}	1825^{15}	-
Pan paniscus	Lomako	-	-	8.0^{4}	-	-	-	-
	Wamba	32.2^{1}	$14.20\ (13\text{-}15)^{4}$	4.50^{4}	-	228^{13}	1460^{9}	-

Data Source:

[1] = Smith and Jungers 1997

[2] = Kappeler and Pereira 2003

[3] = Pusey *et al.* 2005

[4] = Carter *et al.* 2008

[5] = Uehara and Nishida 1987

[6] = this study

[7] = Wich *et al.* 2004

[8] = Robbins *et al.* 2004

[9] = Ross 1988, 2004

[10] = Nishida *et al.* 2003

[11] = Harvey *et al.* 1987

[12] = Barelli *et al.* 2007 (data for Khao Yai)

[13] = Ross and Jones 1999

[14] = Treesucon 1984 (data for Khao Yai)

[15] = Boesch and Boesch-Achermann 2000

[16] = Stumpf 2007

[a] = mean weaning age

[b] = length of the juvenile period was the time between weaning and mean female age at first reproduction (Ross and Jones 1999)

reproduction follows natal dispersal. The interpretation is in line with results on the ovarian function of subadult females having irregular ovarian cycles when females were still in their natal groups (Barelli *et al.* 2007; age estimates at the time of ovarian function monitoring: Hima, 10.25 yr; Rung, 10.33 yr).

Our age at first reproduction for Khao Yai females sharply contrasts with data from captivity where first parturition occurred at 6–8 yr, or even 5 yr of age (*cf.* Geissmann 1991). Perhaps limited breeding opportunities were responsible for a late age at first reproduction in our population. However, because few matured females remained in the study population and comprehensive endocrinological data on sexual maturation of subadult females are lacking, the hypothesis must await further investigation. Alternatively, the difference may reflect perhaps a higher quality and more reliable resource flow in captive environments vs. the natural habitat. However, Savini *et al.* (2008) found no support for a relationship between variation in food availability and female reproductive performance, suggesting that wild Khao Yai white-handed gibbon female reproduction is not particularly food limited. Hence circumstantial evidence suggests that Khao Yai gibbon females may display a typical onset of reproduction whereas captive females may be accelerated in the onset of reproduction, as noted also in other captive primates (Altmann and Alberts 2005; Knott 2001; Masters and Markham 1991).

Primary reasons for a late age at first reproduction of great ape females seem to be slow somatic (Kirkwood 1985) and brain growth (Deaner *et al.* 2003). In other words, a late start of female reproduction in great apes results from positive selection for a prolonged juvenile period, when an important portion of brain development occurs.

Length of Juvenile Period

When we calculated the juvenile period for Khao Yai gibbons, a long span of 9.5 yr emerged, which not only considerably surpasses juvenile periods of similar-sized monkeys but also those of other apes (Table III). Joffe's (1997) calculation of white-handed gibbon juvenile period is similar, which suggests that Khao Yai gibbons are probably not unusual. One might explain the extraordinary long juvenile period in gibbons vs. that of other apes by the earlier age at which offspring are weaned (Table III). However, ultimately it remains difficult to explain why gibbons retained a costly hominoid trait of an extended juvenile period (Begun 2004; Kelley 1997, 2004) that results in individuals who spend between a third and a fourth of their lives inexperienced and unable to reproduce.

Gestation, Weaning Age, and Interbirth Interval

Published data on gestation and lactation periods in gibbons are similarly difficult to interpret. In absolute terms, the periods are intermediate between same-size monkeys and great apes (Table III), but in relative terms the phases are unexpectedly long for the small body mass of gibbons (*cf.* Ross 2004). Similarly, interbirth intervals between surviving offspring were twice as long and longer in Khao Yai gibbons than in similar-sized monkeys, though they ranged at the fast end of the birth spacing continuum in great ape females (Table III).

Before accepting long birth spacing as yet another life history trait that allies gibbons with great apes, it is necessary to evaluate our findings in the context of population variation. Our data closely agree with those on wild Gunung Palung agile gibbons (Mitani 1990); however, longer and shorter intervals occur for white-handed gibbons at Kuala Lompat, Malaysia (10 yr: Chivers and Raemaekers 1980) and Ketambe, Indonesia (22 and 31 mo: Palombit 1995) and even shorter intervals occur in captivity (Geissmann 1991). Compared with previous studies, our sample is larger and, we believe, representative for Khao Yai. But how representative are the data for the species? Interbirth intervals at Khao Yai could be particularly long owing to unfavorable resource conditions that constrain females to space consecutive births unusually widely as occurs in some primates (Knott 1999; Koenig *et al.* 1997). We consider a scenario that attributes long birth interval to poor resources unlikely because high infant survival at Khao Yai indirectly argues against poor food availability or quality and gibbon territory quality appears to be good for most study groups (Savini *et al.* 2008).

Gibbon Life History

It seems clear from our and other studies that gibbon life histories differ considerably from those of monkeys of similar body mass but resemble those of great apes, despite an enormous body size difference. In absolute terms, female age at first reproduction, the duration of gestation and lactation periods, interbirth intervals of gibbons are long, and the juvenile period is slightly longer in gibbons than it is in great apes. In relative terms, when one takes body mass into account, the traits are all as extended in gibbons as they are in great apes when compared to the rest of the primates (Ross 2004). Hence, our findings support the view that apes, gibbons included, collectively have a unique life history, which perhaps foreshadows the unique hominin life history (Kaplan *et al*. 2000).

But why would gibbons have extended life histories? Slowing down the life cycle comes with a cost of also slowing female reproductive rates (Charnov 1991), and late female age at first reproduction profoundly affects female fecundity and population size (Ross and Jones 1999). In great apes, such disadvantages may, at least partly, be offset by a long life span that includes an extended reproductive period (Kappeler and Pereira 2003). However, the crucial benefit of an extended life history, likely derives from an increased potential for cognitive solutions to socioecological challenges (Povinelli and Cant 1995; van Schaik *et al.* 2004). Thus, researchers have interpreted the slow life history trait as a passive consequence of positive selection for an increase in brain size in primates, and by implication, cognitive capacities (Kelley 2004). Such an evolutionary trajectory became possible because great ape ancestors evolved large bodies that allowed for a slowdown of postnatal somatic growth during early life stages without jeopardizing the availability of resources to support the sensitive development of a larger brain (*cf.* Deaner *et al.* 2003). With a large body mass, great ape females are buffered against resource fluctuation and can continuously provide adequate nutrients for their slow-growing infants. A large body mass probably also reduced vulnerability to predation, which in turn positively influenced offspring survival rates (van Schaik *et al.* 2004).

Gibbons do not easily fit such a model. They probably live shorter lives on average than great apes do (Harvey *et al.* 1987), and they might be secondarily reduced in size (Begun 2004; Gebo 2004). Because of their small body mass, it seems that gibbons must suffer higher costs from a slow life course than great apes and humans do. Because a late start of first reproduction may strongly influence female fecundity, it seems that gibbon females would suffer compressed reproductive output vs. those of great ape females, suggesting that slow offspring maturation could probably be maintained only under positive selection pressure. However, a relative loss of reproductive years may be compensated by high offspring survival, which indeed we found in the Khao Yai population (Table III).

A scenario that explains how gibbons perhaps retained a slow life history inherited from a stem hominoid ancestor may be as follows. Instead of growing a larger body, gibbons became smaller and perhaps shielded high predation risks during a slow maturation phase by becoming more cryptic, i.e., living in smaller core social units and by being more secretive (Reichard 1998; Uhde and Sommer 2002). Small size and versatile suspensory locomotion brought about another benefit, because it allowed gibbons to efficiently exploit high-quality resources, i.e., ripe fruit, at difficult to reach terminal ends of branches (Ellefson 1974; Grand 1972). Via a high-quality diet gibbons may have been able to achieve the constant flow of energy that is needed to afford slow offspring maturation, including growth and maintenance of physiologically expensive brain tissue (Aiello and Wheeler 1995). The low infant mortality until weaning age as documented in our sample is perhaps the most convincing indirect argument at hand for the effectiveness of gibbon parental investment. Though the absolute brain volume of gibbons is similar to that of monkeys, their relative brain size falls on the trend line with other apes (MacLeod 2004), and despite reduction in body size, their brains remained larger than expected for a primate of this body mass (Ross 2004), with several areas remaining expanded vs. those of monkeys (Begun and Kordos 2004; MacLeod 2004; Ross 2004) and a neocortex ratio that clusters with great apes (Rilling and Insel 1999).

We can only speculate if gibbons benefit cognitively from an extended life history comparable to that of great apes. Gibbons master simple cognitive tasks (Cunningham *et al.* 2006; Scheumann and Call 2006) and they probably recognize themselves in mirrors (Ujhelyi 2000), but too little is yet known about their cognitive capacities to draw conclusions. Perhaps learning travel routes and the spatiotemporal distributions of foods (Di Fiore and Suarez 2007; Milton 1981, 1988) are important during juvenile years. Contrarily, the preferred foods of gibbons consist mostly of small-to-medium-size berries that can be swallowed whole (Ellefson 1974), and researchers have detected no extractive foraging (Parker and Gibson 1979) or complex manual skills as observed in chimpanzees, gorillas (Byrne 2004; Stokes and Byrne 2001), and orangutans (van Schaik *et al.* 2003).

Alternatively, social skills and competence may need time to develop during juvenile years (Cords and Aureli 2003; de Waal 1993; Joffe 1997), though gibbon societies with their negligible group size variation seem to lack the kind of social complexity predicted to trigger brain evolution (Aiello and Dunbar 1993; Dunbar 1992, 2003; Kudo and Dunbar 2001). However, despite small group size, traditional views of social lives of wild gibbons are changing (Barelli *et al.* 2007, 2008a; Bartlett 2007; Lappan 2007b; Reichard in press), which was also apparent during our study.

Individuals are rarely exclusively pair-living with one partner. Instead, most adults seemingly experience serial partnerships with successive partners and at times also live in multimale groups. Multimale groups are a viable alternative at Khao Yai to the well-documented pair-living social organization of gibbons. Sexual partnerships appear similarly flexible and include polyandrous mating strategies for both pair-living females and ones living in multimale groups. Thus, from our long-term data a picture of social complexity materializes that has so far rarely become visible in gibbon societies. An important component of social flexibility is expressed in a variable choice of social and mating partnerships. To assess if the flexibility in Khao Yai gibbon females is comparable to that in great apes, we follow van Schaik *et al.* (2004) to evaluate how Khao Yai gibbons may share aspects of great ape sociality.

The Complexity of Gibbon Social Life and Female Reproductive Strategies

Van Schaik and colleagues (2004: 199 ff.) argued that great apes are united as a group by subtle social commonalities (points 1–4 below), which, together with a slow life history, form the basis for their exceptional cognitive evolution. We now consider which social commonalities gibbons share with great apes (*sensu* van Schaik *et al.* 2004):

1) *A tendency toward fission-fusion social organization (or at least toward facultative social units), with individuals out of contact with conspecifics for prolonged periods and with foraging females notably solitary.* Like other apes, gibbon females forage independently of each other. However, no tendency toward a flexible choice of association partners or group membership similar to that of chimpanzees or bonobos is evident. Social units of white-handed gibbons, like those of gorillas, are spatially cohesive (Bartlett 2007; Chivers 1971), though intergroup encounters between neighboring groups are common in several gibbon species and show variable individual participation (Bartlett 2003; Reichard and Sommer 1997; Sommer and Reichard 2000) and sometimes involve the members of ≤4 groups (Reichard, *pers. obs.*). Fuentes (2000) proposed that gibbon societies are effectively communities, in which neighboring individuals interact flexibly and frequently with each other. However, overall, too little is known yet about social interactions between groups to evaluate the community model. To date, it seems safe only to notice that gibbon females, like other ape females, forage independently of each other and that stronger evidence for flexible associations must await further studies.

2) *Relatively high subordinate leverage*. Subordinate leverage would be reflected in an absence of formal dominance despite a potential for clear-cut contest competition (van Schaik *et al.* 2004). In gibbons, male-female relationships are commonly characterized by codominance (Carpenter 1940; Leighton 1987), which indicates that neither sex has obvious power over the other, which is at least partly a consequence of their sexual monomorphism (*cf.* Plavcan 1999; Plavcan *et al*. 1995). Formal dominance signals are absent between the sexes, and likewise between females or between males as evidenced during intergroup encounters or in polyandrous groups, wherein the potential for clear-cut contest competition would be greatest but social tolerance seems to prevail (Barelli *et al.* 2008b; Reichard in press). Overall, gibbons conform to the pattern van Schaik *et al.* (2004) described for great apes but with the important caveat that the potential for dominance signals is lower in gibbons than in most great apes given their small group size and thus a limited number of intrasexual relationships.

3) *Intrasexual bonds among nonrelatives are as common, or more so, than bonds among relatives*. Most gibbon populations have been characterized by long-term social

stability, but we have witnessed more adult member changes at Khao Yai than in any other gibbon population (Barelli *et al.* 2008a; Savini *et al.* 2008). Compositional changes were repeatedly due to male immigration (Reichard in press) and often resulted in nonrelatives living together for prolonged times, i.e., ≥2 yr. Brockelman *et al.* (1998) described social relationships in one such group as harmonious. In multimale groups at Khao Yai, the males sometimes groomed each other and there were tendencies of males to engage simultaneously in intergroup encounters (Savini *et al.* submitted). Hence, preliminary observations do not contradict the idea that gibbon nonrelatives establish bonds. Contextual flexibility in gibbon social relationships is underscored by tolerance between males in multimale groups vs. male-male interactions during intergroup encounters that are generally agonistic (Reichard and Sommer 1997).

4) *Remarkably extensive intraspecific flexibility in social organization and affiliation*. Our focal gibbons strongly expressed flexibility in social organization (Kappeler and van Schaik 2002). Besides a predominance of pairs, multimale groups (usually 2 adult males and 1 female) were common and sometimes long-lasting. Flexibility in association patterns was further expressed in instances of multifemale groups, i.e., coresidence of 2 unrelated females. Based on our long-term records, we conclude that individuals at Khao Yai are likely to experience different living arrangements throughout their reproductive lives. Female mating strategies are likewise flexible. On reaching sexual maturity, females develop moderate sexual swellings (Barelli *et al.* 2007), which likely evolved in the context of promiscuous mating systems (Nunn 1999; Zinner *et al.* 2004), and overall gibbon females mate polyandrously with males living in their immediate vicinity (Barelli *et al.* 2008a; Reichard 1995).

In summary, our and other recent gibbon studies (Barelli *et al.* 2007, 2008a; Bartlett 2003, 2007; Lappan 2007b; Reichard 2003; Savini *et al.* 2008; Sommer and Reichard 2000) suggest that gibbons exhibit social commonalities compatible to those of other apes, though they express some traits less. Such variation is not surprising given the great diversity in social systems and ecology of apes that leads to different preconditions, potentials, and cost-benefit equations for the expression of the flexibility-trait in particular domains.

Conclusion

We conclude that social flexibility is well represented in the gibbons and thus unifies all apes. The implications of our findings are significant in light of theories linking life histories, complex female reproductive strategies, and flexible social associations to the evolution of primate cognition.

One plausible scenario is that gibbons inherited the traits from a larger stem hominoid, and though they became secondarily smaller (Begun 2004; Ward *et al.* 2004), they retained slow life histories and flexible female reproductive strategies. Because effective predation avoidance seems a crucial obstacle when offspring mature slowly (Janson and van Schaik 1993), we believe increased infant survival is the driving force behind the maintenance of slow life histories and suggest that gibbons decreased predation vulnerability via an entirely arboreal lifestyle, a secondary reduction in group size, and an effective top-speed, high-canopy locomotion style that makes them nearly immune to a variety of potential predators. Concomitantly, the efficient locomotion of gibbons allowed them to exploit effectively a high-quality feeding niche of forest fruits that was likewise crucial to retain a slow life history.

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