GROWING UP GIBBON

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I. INTRODUCTION

Hylobates is a successful genus of specialized fruit-eating, small-bodied apes that inhabit the tropical rainforests of Southeast Asia. Adolph Schultz (1944) described growth of wild white-handed Hylobates lar and highlighted somatic changes through the life stages. His study remains one of the few analyses available on gibbon anatomical growth and development.

In a new study, we revisit the A.P.E. gibbon collection (Ankga series), housed at the Museum of Comparative Zoology, Harvard University. Schultz's excellent field notes and specimen preservation allowed us to build on, revise, and add to his work. We incorporate dental-aging techniques and revise age class determinations to reconsider the growth pattern of the brain, dentition, skeleton, and body mass in immature gibbons. The physical evidence, coupled with long-term behavioral research of extant *H. lar*, are the bases for reassessment of anatomical growth within a chronological and behavioral framework (e.g., Dirks and Bowman, 2007; Reichard et al., 2012). We propose new interpretations of gibbon growth and life history.

II. MATERIALS AND METHODS

The *Hylobates lar* specimens were collected during the 1937 Asiatic Primate Expedition in a few short months in a limited geographical region in Thailand and represent a unique data set. Schultz recorded notes in the field on each individual, for example, the size of mammary glands in the sub-adult/adult females, and whether or not females were pregnant and/or were nursing.

The immature sample consists of 48 individuals (27 female, 21 male) collected in the Ankga region, assessed for body mass and trunk height in the field, and in the lab for long bone lengths, tooth eruptions, bone fusions and cranial capacities (after Schultz, 1944). In the lab we also assessed bone fusions and tooth eruptions to assign age class categories, and measured cranial capacities and diaphyseal long bone lengths (after Bolter and Zihlman, 2003). These immatures were compared with 92 adults from Ankga and Chiengmai regions (42 female, 50 male) for mass and length measurements taken in the field. Not all measurements are available for all specimens.

TABLE 1. Sample

Age Class (Life Stage)	Teeth erupted	Estimated age range in years	Sex and Sample Size
1 (Infant)	Deciduous only	.42 – 1.7	F 3 M 5
2 (Juvenile)	M1s	1.8*– 3.7 (?)	F 8 M 2
3 (Juvenile)	M2s	3.8 (?) – 6.0	F 8 M 8
4 (Sub-Adult)	M3s	> 6.1	F 8 M 6
5 (Adult)	M3s (humerus fused)	> 6.1	F 42 M 50

*estimated by Schultz (1944) based on one captive infant with approximated birth date

We categorized immatures into 4 age classes by molar eruption sequences and skeletal fusion (after Bolter and Zihlman, 2003). Sub-adults had all molar teeth erupted, but no proximal humeral fusion (Table 1).

These age class categories are modified from Schultz (1944), who assigned Juvenile 1 based on a mixture of deciduous and adult teeth, and Juvenile 2 when only permanent teeth were present, and did not include skeletal fusions in age class assignments. Based on these revised categories, we reclassified 7 females and 6 males as sub-adults that were adults to Schultz. Estimated age ranges in years are taken from mandibular deciduous and permanent molar eruption schedules (Schultz, 1944; Rumbaugh, 1965; Smith et al., 1994; Dirks and Bowman, 2007; Dirks et al, 2013).

III. RESULTS

Results highlight individual features by age class (Table 2).

- Age class 1 infants (~4-21 months) females have diaphyseal intermembral indices of 127.2, close to the adult intermembral average of 130.2; and infant males have 126.9 compared to 131.4 of adults. These proportions stay constant through the life stages.
- Age class 2 juveniles (~1.8 – 3.7? years) have attained over 90% of the brain size of the adult averages; body mass averaged between 23-33% of adult values, and trunk height 66-67% of adult values.
- Age class 3 juveniles (~3.8? – 6.0 years) double the body mass of age class 2, reaching slightly over 50% of average adult body mass. In trunk length, females average 84% of adults and males 87%.
- Age class 4 sub-adults (at least ~6.1 yrs) have all of their permanent teeth; body growth is incomplete (bones unfused) and sex differences appear. Females average 93.1% adult body mass and 97% trunk height and are not significantly different than adult females. Males average 88.6% body mass and 90% trunk height and are significantly different from adult males.

IV. DISCUSSION

Reassessing age class categories in the A.P.E. gibbon collection at Harvard's MCZ reveals subtle distinctions in gibbon stages of life history, particularly in females reaching somatic adulthood long before reproducing, and in males exhibiting a different growth pattern than females in the sub-adult period.

Schultz apparently was aware that there was a gap between the time a female had all her permanent teeth and when she first reproduced. He noted:
"all females showing no, or very slight wear of the teeth had extremely small mammary glands, mere button-like nipples, and were neither pregnant nor nursing any babies. It seems, therefore, that female gibbons may not become fertile until some time after they have attained adulthood" (1944, 10).

The addition of long-term field research on gibbons confirms Schultz's hypothesis. In Khao Yai National Park in Thailand research on 14 white-handed gibbon groups documents the highly protracted nature of *Hylobates lar* growth and development: age at weaning, between 2.0-2.5 years; age of first female reproduction, 10.5 + 1.2 years (Reichard et al, 2012). Female gibbons spend about 7 years as juveniles/subadult before having their first offspring.

Our study indicates a sex difference in life history. Females have obtained adult body mass and trunk length by third molar eruption ~6.1 years, whereas males have not. Hence, factors other than diet (e.g., frugivory) appear to affect the timing of dentition and body development (see Leigh, 1994; Dirks and Bowman, 2007). This sex difference may be a generalized catarrhine pattern wherein females reach adult weight and height with full permanent dentition, whereas males do not (Bolter and Zihlman, 2003). Gibbon males continue to add considerable body mass and trunk length during a sub-adult phase. The timing (or duration) of sub-adulthood appears to vary among monkeys and apes but the pattern of females maturing first in a species appears consistent in gibbons as with other catarrhines (Bolter and Zihlman, 2003; Bolter, 2004; Zihlman et al, 2007).

What might account for this long period between weaning and first reproduction in gibbons? One other ape has this extended life history, with about 7 years from weaning to reproduction: the orangutans. Field researchers suggest that orangutans may need this longer time to establish ecological competence (van Noordwijk and van Schaik, 2003). Gibbons, like orangutans, inhabit the Southeast Asian rain forests that have periodic and irregular abundance of fruit in mast fruiting events, and relatively low productivity in the intervening time (Knott, 1998).

During these low fruit periods, gibbons depend upon finding the small fruit patches widely scattered in their range. Their locomotor system enables speedy travel to several patches a day and their small body size can take advantage of sources that larger-bodied species cannot (MacKinnon, 1977). It is possible that for gibbons to master locomotor and cognitive skills of finding pathways and food sources they require extended time with adults prior to leaving the natal group, finding a mate and setting up a new territory.

V. SUMMARY AND CONCLUSIONS

1. Gibbons have a slow life history, evidenced in both anatomical and behavioral development.

2. Female gibbons reach adult body mass and trunk height before males of comparable dental/skeletal age.

3. Female gibbons spend nearly 10 years in infant/juvenile/sub-adult life stages before reproducing, although body mass and trunk height are mature after about 6 years.

4. The protracted growth and development in gibbons is similar to that of orangutans, who also spend 7 years after weaning in a juvenile/sub-adult (pre-reproductive) life stage.

5. Ecological competence requiring locomotor and cognitive skills in the irregular food sources of SE Asian rainforests may have selected for protracted life history in gibbons.

TABLE 2. Measurements by revised age classes

Age Class (Life Stage)	Body mass kg (range)	Trunk height mm (range)	Cranial capacity ml (range)	Intermembral index-diaphysis (range)
1 (Infant)	F: .60 (.45-.68) M: .64 (.45-.78)	F: 130.3 (123-139) M: 134.3 (122-143)	F: 88 (80-98) M: 83 (77-98)	F: 127.7 (125.7-130.0) M: 126.9 (122.6-129.8)
2 (Juvenile)	F: 1.78 (1.13-2.50) M: 1.36 (1.36)	F: 183.5 (163-210) M: 180 (180)	F: 93.1 (72-108) M: 97.5 (85-110)	F: 130.3 (125.0-134.8) M: 128.8 (128.3-129.2)
3 (Juvenile)	F: 3.01 (2.27-3.86) M: 3.36 (2.04-4.08)	F: 228.7 (212-242) M: 235.2 (195-269)	F: 95.9 (88-106) M: 93.6 (85-114)	F: 129.0 (126.6-134.1) M: 132.8 (127.2-137.3)
4 (SubAdult)	F: 4.99 (4.08-5.90) M: 5.17 (4.08-6.35)	F: 265.0 (248-279) M: 245.5 (234-258)	F: 105.8 (96-114) M: 113.3 (96-125)	F: 133.2 (130.0-137.3) M: 136.1(129.0-140.4)
5 (Adult)	F: 5.36 (3.80-6.80) M: 5.83 (4.08-7.37)	F: 272.5 (245-279) M: 271.3 (254-293)	F[1]: 103.3 (90-116) M[1]: 105.8 (92-118)	F[2]: 130.2 M[2]: 131.4

[1] from Schultz field notes, Chiengmai and Angka *H lar*
[2] from Schultz 1944; Chiengmai *H lar* on total long bone lengths

Infant Juvenile 1 Juvenile 2 Sub-adult

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