Hylobatid Communities: Changing Views on Pair Bonding and Social Organization in Hominoids

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ABSTRACT   Social organization involving pair bonding and two-adult groups is rare in mammals. Current sociobiological theory suggests that this grouping and behavior pattern is somewhat anomalous. The gibbons (genus *Hylobates*) are the only hominoids to exhibit pair bonds and two-adult groups. In this article I present an overview of the current issues in monogamy and pair-bond theory, and review traditional conceptualizations and the accumulated data relevant to gibbon social organization. The significance of hominoid behavioral phylogeny and population-wide studies is also considered.

Recent findings indicate that pair-bonding and two-adult groups are not ubiquitous among the hylobatids. Many aspects of gibbon behavior and ecology do not conform to expectations of the conditions under which two-adult groups and/or pair-bonding patterns should evolve. A review of the information available from long-term and short-term studies of gibbons suggests an alternative way of viewing their socioecology. I propose that gibbons currently exist in variable communities that have arisen via ecological pressures and specific behavioral patterns from an ancestral multimale/multi-female grouping pattern. This social organization is not best characterized as "monogamous." This review also suggests that hominoid grouping patterns can be viewed as occurring along a continuum rather than as being discretely different units. Yrbk Phys Anthropol 43:33–60, 2000.   © 2000 Wiley-Liss, Inc.

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THE PROBLEM OF "MONOGAMY"

If female mammals exhibit an overall larger investment in each offspring than males and are limited by resource distribution, males are then limited by the distribution of females (Williams, 1966; Trivers, 1972). Given this limitation, males must compete for females and their reproductive success is therefore closely related to the number of females that they can fertilize (Wilson, 1975; Wrangham, 1979). Within this scenario it is expected that few, if any, species would exhibit social systems in which males "restrict" themselves to only one female and thus reduce their potential reproductive success (Wilson, 1975; Wrangham, 1979). The order Primates is generally held to have a relatively high percentage of these one-male/one-female grouped, or "monogamous," species and is thus a good arena for investigating the evolution of such systems (Kinzey, 1987; Kleiman, 1977; Rutberg, 1983).

Monogamy is generally defined as "a prolonged association and essentially exclusive mating relationship between one male and one female" (Wittenberger and Tilson, 1980). However, other associated concepts, behavior, and character states are frequently included in functional definitions of "monogamy" in primates. The most pronounced of these concepts are the "family unit" and "pair bond," which revolve around the same key element: a special and exclusive relationship between an adult male and an adult female. The idea of the monogamous family unit is also accompanied by assumptions of mate fidelity and mate guarding. Other elements included in the primate "monogamy package" are sexual monomorphism in body size, territoriality, genetic relatedness of offspring to adults = 0.5 (both adults in the group are the parents of the offspring), joint vocal or visual displays (or other bond-reinforcing behavior)

by the adults, and repulsion of same-sex intruders from the group's territory (Anzenberger, 1992; Kleiman, 1977; Rutberg, 1983; van Schaik and Dunbar, 1990; Wittenberger and Tilson, 1980).

Until recently it was proposed that although only approximately 3% of nonprimate mammalian species were "monogamous," up to 15% of primates were (Kleiman, 1977; Rutberg, 1983; Kinzey, 1987). Recent research and reviews (see Fuentes, 1999a) have demonstrated that the number of primate species occurring in two-adult bisexual groups is lower than 15% and closer to rates that seem to characterize mammals on the whole. Of the 49 species of primates previously termed "monogamous" (Table 1), only a maximum of 8–21 (~3–8% of total primate species) (Table 2) occur primarily in two-adult groups throughout their range (Fuentes, 1999a,c, 2000). These two-adult species vary in group size, activity patterns, body size, dietary patterns, range size and use, territoriality, mating patterns, group tenure patterns, intra-adult behavior patterns, and phylogenetic and geographic distribution (French and Schaffner, 1999; Fuentes, 1999a,c, 2000). The primate species that do occur in two-adult groups do not necessarily reflect the same evolutionary pressures (French and Schaffner, 1999; Fuentes, 1999a,c, 2000). Given what we know about the primate species that occur in one-male/one-female groups, it is safe to say that there is no uniform social organization called "monogamy" (French and Schaffner, 1999; Fuentes, 1999a).

However, this knowledge has not reduced the keen interest in "monogamy" and two-adult groups in primates. This marked interest may be due in part to the attention two-adult grouped primates draw due to their assumedly "derived" or aberrant state relative to other grouping types (Hrdy, 1981; Kinzey, 1987). The "derived anomaly"

TABLE 1. Nonhuman primate species which have had labeled "monogamous"[1]

Prosimians		
Cheirogaleidae	*Indriidae*	*Lemuridae*
Phaner furcifer TG	*Avahi laniger* TG, M	*Eulemur rubriventer* TG, M
Lepilemuridae	*Indri indri* TG, M	*Eulemur mongoz* TG, GTG, M, P
Hapalemur aureus TG	*Propithecus diadema* GTG, P	*Varecia variegata* GTG, P
Hapalemur griseus GTG	*Propithecus tatersalli* GTG, P	
	Propithecus verrauxi GTG, P	
	Tarsiidae	
	Tarsius bancanus GTG	
	Tarsius spectrum GTG	

Anthropoids		
Callitrichidae	*Cebidae*	*Cercopithecidae*
Callimico goeldii GTG, P, M	*Aotus trivirgatus* TG, M	*Allenopithecus nigrivoides* GTG, P
Callithrix humeralifer GTG, P, M	*Aotus nigriceps* TG, M	*Cercopithecis hamlyni* GTG, P
Callithrix jacchus GTG, P, M	*Callicebus moloch* TG, M	*Cercopithecus neglectus* TG, GTG, P
Cebuella pygmea GTG, P, M	*Callicebus personatus* TG, M	*Presbytis potenziani* TG
Leontopithecus chrysomelas GTG, P, M	*Callicebus troquatus* TG, M	*Simias concolor* TG, GTG, P
Leontopithecus rosalia GTG, P, M	*Pithecia albicans* GTG, P	*Hylobatidae*
Saguinus fuscicollis GTG, P, M	*Pithecia monachs* GTG, P	*Hylobates agilis* TG, M
Saguinus imperator GTG, P, M	*Pithecia pithecia* GTG, P	*Hylobates concolor* TG, GTG, M, P
Saguinus labiatus GTG, P, M	*Pithecia irrorata* GTG, P	*Hylobates hoolock* TG, GTG, M
Saguinus mystax GTG, P, M		*Hylobates klossi* TG, GTG, M
Sagiunus nigricolis GTG, P, M		*Hylobates lar* TG, GTG, M, P
Saguinus oedipus GTG, P, M		*Hylobates moloch* TG, M
		Hylobates muelleri TG, M
		Hylobates pileatus TG, GTG, M, P
		Hylobates syndactylus TG, GTG, M, P

[a] Compiled from Kinzey, 1987; Kleiman, 1977; Rutberg, 1983; Smuts et al., 1987; van Schaik and Kappeler, 1993; Wittenberger and Tilson, 1980, and as summarized in Fuentes 1999a, 2000; and Sussman, 1999, 2000. TG, two-adult groups; GTG, greater-than-two-adult groups; M, monogamous mating pattern; P, polygamous mating pattern.

status combined with a strong cultural association in Western classical society and Judeo-Christian traditions make "monogamy" very interesting to both the evolutionary theorist and the individual searching for explanations of our current moral and social systems (Hrdy, 1981; Symons, 1979; Wrangham et al., 1999).

Instead of attempting to force primates that occur in one-male/one-female groups into a single type of social organization, I recently proposed two categories (Fuentes, 1999a). The *two-adult group* is a demographic label describing species that occur primarily in one-male/one-female groups throughout their range. The *pair-bonded group* describes species that are in two-adult groups *and* exhibit a specific and quantifiable set of pair-bond behavior. Few of the species that occur in *two-adult* groups can be said to occur in *pair-bonded* groups (Fuentes, 1999a,c, 2000). Under these divisions, the term "monogamy" is only used to refer to a specific mating pattern where one male and one female mate exclusively for at least one reproductive/seasonal cycle.

PAIR BONDS AND TWO-ADULT GROUPS

The "pair bond" is becoming, for some, the basal unit of social organization in many primate taxa. Several authors propose the pair bond as the central aspect in models of the evolution of lemur, gibbon, and human societies (Jolly, 1998; van Schaik and Kappeler, 1997; Lovejoy, 1981; Palombit, 1999; Wrangham et al., 1999). This focus on the pair bond is primarily rooted in the search for its evolutionary or functional origins, the manner in which selection pressures may have "produced" pair bonds, and how pair bonding relates to individuals' genetic fitness (see Rasmussen, 1981). As such, the pair bond is a critical element in the current examination of the evolution of primate social organization. Despite its frequent use

TABLE 2. Primate species that occur in two-adult, or pair-bonded, groups throughout their range[1]

	Body size: Male	Body size: Female	Activity pattern	Group size	Distribution
Lemuridae					
Eulemur rubriventer	1,800–2,400 g	1,650–2,220 g	Cathemeral	2–4	Madagascar
Hapalemur aureus	1,540–1,660 g	1,500 g	Diurnal	2–4	Madagascar
Cheirogaleidae					
Phaner furcifer[2]	460 g	460 g	Nocturnal	2–5 or solitary	Madagascar
Indriidae					
Avahi laniger[2]	900–1,200 g	1,200–1,600 g	Nocturnal	2–5	Madagascar
Avahi occidentalis[2]	900–1,200 g	900–1,200 g	Nocturnal	2–5	Madagascar
Indri indri	5,750–5,900 g	6,750–7,520 g	Diurnal	2–4	Madagascar
Cebidae					
Aotus trivirgatus	950 g	920 g	Nocturnal	2–5	So America
Aotus nigriceps	825–1,050 g	780–1,100 g	Nocturnal	2–5	So America
Callicebus moloch	800–1,200 g	700–1,020 g	Diurnal	2–5	So America
Callicebus personatus	1,050–1,650 g	970–1,600 g	Diurnal	2–6	So America
Callicebus torquatus	1,100–1,500 g	1,151–1,462 g	Diurnal	2–6	So America
Cercopithecidae					
Presbytis potenziani[2]	6,500 g	6,400 g	Diurnal	2–6	SE Asia
Hylobatidae[3]					
Hylobates agilis	5,550–6,400 g	5,550–6,400 g	Diurnal	2–7	SE Asia
Hylobates concolor	4,500–9,000 g	4,500–9,000 g	Diurnal	2–11	S/SE Asia
Hylobates hoolock	6,900 g	6,100 g	Diurnal	3–6	S Asia
Hylobates klossi	5,800 g	5,800 g	Diurnal	2–9	SE Asia
Hylobates lar	4,970–7,600 g	4,400–6,800 g	Diurnal	3–12	SE Asia
Hylobates moloch	5,700 g	5,700 g	Diurnal	3–4	SE Asia
Hylobates muelleri	5,000–6,400 g	5,000–6,400 g	Diurnal	2–5	SE Asia
Hylobates pileatus	7,860–10,450 g	6,360–8,640 g	Diurnal	2–5	SE Asia
Hylobates syndactylus	12,270–14,770 g	10,000–11,140 g	Diurnal	2–10	SE Asia

[1] From Fleagle, 1999; Fuentes, 1999a; Rowe, 1996; Sussman, 1999, 2000. S, South; So, South; SE, Southeast.
[2] These species lack long-term studies that would enable us to confirm whether or not they occur in two-adult groups throughout their range.
[3] Many gibbon species have been reported as occurring in larger-than-two-adult groups.

as a descriptive term and its critical role in theoretical reconstructions of the evolution of social organization, there are few specific definitions or descriptions of what a "pair bond" is.

In the primatological (and greater zoological) literature there is a general consensus that bonds between adults are best described as predictable relationships that can be assessed by rates of affiliative interaction, proximity scores, and a measure of reciprocity between two individuals (Hinde, 1983; Krebs and Davies, 1997). In the examination of two-adult groups I propose that we focus on measuring social pair bonds which are defined as long-term associations between two nonkin adults that are characterized by a set of partner-specific affiliative behaviors and energetic investment patterns (Fuentes, 1999a,c, 2000).

Recent reviews (Fuentes, 1999c, 2000) demonstrate that two-adult grouped primates have a distinct geographical distribution (see Table 2). There are no two-adult grouped primates on the African continent

and only two types in all of Asia (*Hylobates* spp. and *Presbytis potenziani*). This may be due to differences in ecological formations, niche availability, and/or different evolutionary trajectories for the African mainland primate forms (Fuentes, 1999c, 2000). There is also a size trend in the two-adult grouped primates: small. Only the two Asian genera and the lemur *Indri* exceed 4,000 g, with the majority being under 2,000 g. Both neotropical genera are small (<1,700 g) and are under heavy predation pressure (Kinzey, 1997; Wright, 1986). All of the two-adult grouped primates are primarily arboreal. This suggests that terrestriality is not compatible with two-adult groups in primates. The geographic and phylogenetic distributions of the two-adult grouped species suggest that this grouping pattern has arisen in at least four, or as many as six, separate evolutionary events.

Strong, overt social pair bonds may not occur in prosimians or nocturnal primates and in fact may be quite rare in primates (however, there are currently insufficient

TABLE 3. Hypotheses put forward related to two-adult and pair bonded primate species

	Is this hypothesis supported by the data available for the hylobatids? (see text)
Foraging	
Food competition or foraging hypothesis (Horn, 1968; Wilson, 1975): group size is adjusted to the distribution and abundance of resources in time and space.	Yes
Females as a limited or widely dispersed resource (Rutberg, 1983; van Schaik and van Hooff, 1983; Wrangham, 1980): resource distribution and/or the related distribution of females limits males' ability to access more than one female effectively.	No
Male defense against predators or defense against resource competition from conspecifics or others (Wittenberger and Tilson, 1980; van Schaik and Dunbar, 1990): females require a bonded males' assistance to defend resources or in vigilance/antipredator behavior.	Yes (in modified form; see text)
Predation pressure	
Predation pressure hypothesis (Crook and Gartlan, 1966; Dunbar, 1988): predation affects group size	No
Male investment strategies	
Assistance rearing offspring hypothesis (Kleiman, 1977): a minimum of two adults are required to successfully raise offspring.	No
Infanticide prevention (van Schaik and Dunbar, 1990; van Schaik and Kappeler, 1997): females must bond with a male to defend against infanticide.	No
Mate guarding	
Mate guarding (Palombit, 1999): heterosexual pair bond is male initiated and derived from a scenario in which by pair bonding with a female any given adult male potentially maximizes his reproductive success (or at least minimizes the variance in his reproductive success).	Yes (in modified form; see text)

data on most species to test this claim; Fuentes, 1999c, 2000). Two-adult groups appear associated with a monogamous mating pattern (see Table 1). However, genetic paternity data and continued long-term investigation into many species' mating patterns may provide new information that contradicts this assertion. It is possible that two-adult groups could arise in a species either via selection for a specific mating system or via pressures on group size and/or number of females. The actual relationship between two-adult groups and monogamy deserves a great deal more specific attention.

A number of hypotheses have been proposed to explain the occurrence of the two-adult group and/or pair bonds in primates. Each of these hypotheses derives from the larger zoological and evolutionary literature and theory (see Table 3). They attempt to provide evolutionary explanations as to why, given anisogamy and differential overall parental investment in sexually reproducing organisms, a species would arrive at a two-adult or pair-bonded social system. Anisogamy refers to the different sizes (and relative energetic cost of) gametes (sperm and egg). Females are "parasitized" by males in the sense that females are producing larger, more expensive gametes and investing more overall energy in the gestation and lactation of young than are the males. Therefore it is considered that a monogamous mating system (assumed to occur in two-adult and pair-bonded groups) reduces the optimum potential of a male's reproductive success due to limits on female productivity. These general explanations rest on the assumption that monogamy is a derived state (at least for males) and that two-adult or pair-bonded primate species exhibit all, or at least many, of the "monogamous" behavioral elements (Fuentes, 1999a; Hrdy, 1981; Kleiman, 1977; Wittenberger and Tilson, 1980).

THE ROLE OF HYLOBATIDS IN "MONOGAMY" AND PAIR-BOND THEORY

The gibbons (genus *Hylobates*) have played a prominent role in the construction of hypotheses for the occurrence of two-adult, pair-bonded, or "monogamous" social organization (Mitani, 1984; Palombit, 1999; van Schaik and Dunbar, 1990; Tilson, 1980; Wittenberger and Tilson, 1980). From some

of the early field studies to some more recent influential studies (Brockelman and Srikosamatara, 1984; Chivers, 1974; Ellefson, 1974; Mitani, 1984), the hylobatids were seen until recently as the "paragons of fidelity," the model family unit, and the standard bearers of the "monogamous" primates. However, as early as 1940 Carpenter warned, "It was found that the gibbon family pattern with limited variations characterized gibbon societies. . . . But this description may be an overgeneralization" (Carpenter, 1940, p. 125). Aside from one little-studied leaf monkey (*Presbytis potenziani*), the gibbons are the only catarrhine primates that occur primarily in two-adult groups throughout their range (Fuentes, 1999a).

By examining the traditional representation of gibbons and contrasting it with the last decade's advances from long-term research, we can revisit long-held assumptions in the light of new data. In doing so we can attempt to create a more comprehensive picture of gibbon sociality and reexamine hypotheses related to the evolution of gibbon societies.

THE GIBBONS—PAST STUDIES

The gibbons, frequently referred to as "lesser apes," are well-known for their unique anatomical, genetic, and behavioral profiles (Preuschoft et al., 1984). Table 4 provides an overview of the major studies on the various gibbon species.

The gibbons (genus *Hylobates*) are divided into between 5–11 species and placed into 3–4 subgenera (Bartlett, 1999b; Leighton, 1987; Morales et al., 1999; Rowe, 1996). Current consensus based on molecular and chromosomal evidence places nine species of gibbons into four subgenera (Bartlett, 1999b; Morales et al., 1999) (see Table 5). The gibbons are characterized by sexual monomorphism in body size. Some species are sexually polymorphic in pelage coloration and a few are asexually polymorphic in this trait. Gibbons range across Southeast Asia from eastern India to southern China and across the Malay peninsula, reaching an eastern extreme on the islands of Borneo and Java in the Sunda region (Preuschoft et

al., 1984). See Figure 1 for the general distribution of species.

Gibbons are found primarily in evergreen rain forests, with some populations living in semideciduous and mixed evergreen seasonal environments in the northern portions of the genus' range (Preuschoft et al., 1984; Rowe, 1996). Forests with gibbons tend to have high tree diversity and frequently a high representation of dipterocarps (Chivers, 1986). Gibbons primarily occur in small, strictly arboreal groups, including two adults and young. Group sizes range from 2–11 (Chivers, 1984; Leighton, 1987; Rowe, 1996; Sheeran, 1993) averaging between 3–5 individuals. The age of first birth is between 6–9 years, interbirth intervals fall between 2.5–5 years, and sexual maturity ranges from 6–10 years of age (Brockelman et al., 1998; Chivers and Raemakers, 1980; Geismann, 1991; Leighton, 1987; Sheeran, 1993). Pair longevity ranges from a few months to over 10 years (Brockelman and Srikosamatra, 1984; Brockelman et al., 1998; Chivers, 1974; Palombit, 1994). There is little evidence for clear dominance relationships within the adult members of a gibbon group (Brockelman et al., 1998; Prueschoft et al., 1984).

It is held that young adult gibbons are forced from their natal groups via aggression from the same-sex parent (Chivers, 1974; Leighton, 1987). As a young gibbon reaches sexual maturity, some authors report increased levels of agonism and even direct physical aggression from the same-sex adult (Chivers, 1974; Leighton, 1987). As peripheralization is increased, the young individual leaves the group and seeks out a nearby vacant territory and/or a solitary individual of the opposite sex (Leighton, 1987). Young adults may approach and remain peripheral to new or neighboring groups, which contain opposite-sex subadults/juveniles in order to attract a mate (Chivers, 1974; Chivers and Raemakers, 1980; Leighton, 1987; Sheeran, 1993; Tilson, 1981). Recent reports, however, suggest that there is more variation in intragroup dynamics between adults and subadults than previously thought, and that there might not be one primary pattern (same-sex exclusion) across all gibbons (Brockelman et

TABLE 4. Summary of Hylobates studies

Species	Location	Duration of study	No. of groups	Mean group size	Density (individuals/km²)	Day range	Home range	References
Hylobates agilis	W. Malaysia	11 months	7	4.4	18.9	1,217 m (650–2,200)	29 ha (n = 1)	Gittins, 1980
Hylobates agilis	W. Kalimantan, Indonesia	19 months	8 (28)[1]	4.1	14.9	NA	NA	Mitani, 1987, 1990
Hylobates concolor	Xiobahe, Yunana, China	8 months	4	5.25	2.6	NA	NA	Sheeran, 1993; Lan and Sheeran, 1995
Hylobates concolor	Hainan, China	60 months	4	5.25	1.8	NA	200–500 ha (n = 4)	Zhene et al., 1989
Hylobates hoolock	Jorhat, Assam, India	62 days	7 (24)[1]	3.2	7	NA	22 ha (18–30) (n = 7)	Tilson, 1979; Gittins and Tilson, 1984
Hylobates hoolock	Tripura, India	2 months	9	3	5	600 m (300–1,000)	300–400 ha	Mukherjee, 1986
Hylobates klossi	Siberut, Indonesia	3 months	11	3.4	24.8	NA	5–8 ha (n = 13)	Tenaza, 1975
Hylobates klossi	Siberut, Indonesia	22 months	2 (10)[1]	3.7	10.4	1,514 m (885–2,150)	31–35 ha (n = 3)	Whitten, 1980
Hylobates klossi	Siberut, Indonesia	21 (10) months[2]	4 (15)[1]	4.1	24.8	NA	8.8–12.5 ha (n = 10)	Tilson, 1981
Hylobates lar	Khao Yai, Thailand	18 years (1,665 days)	4 (12)[1]	4.3[3]	34.4[3]	1,245 m (672–1,791)	21–40 ha (n = 12)	Brockelman et al., 1998; Bartlett, 1999; Reichard, 1995
Hylobates lar	Kuala Lompat, Malaysia	12 months	6	3.3	2	1,490 m (450–2,900)	50–58 ha (n = 2)	Gittins and Raemakers, 1980
Hylobates lar	Tanjong Triang	15 months	4	3.3	6.6	NA	59 ha (n = 4)	Ellefson, 1974
Hylobates lar	Ketambe, Sumatra, Indonesia	72 months	3 (7)	4.1	4.7	NA	NA	Palombit, 1992, 1994a
Hylobates lar	Doi Dao, Thailand	3 months	21	4.3	NA	NA	16–32 ha (n = 3)	Carpenter, 1940
Hylobates moloch	Ujung-Kulon, West Java, Indonesia	11 months	6 (31)[1]	3.3	8.9	1,400 m	11.9–22 ha (n = 6)	Chivers, 1984; Kappeler, 1984
Hylobates muelleri	Kutai, Kalimantan, Indonesia	15 months	7	3.4	10.2	850 m (350–1,890)	33–43 ha (n = 6)	Leighton, 1987
Hylobates pileatus	Khao Soi Dao, Thailand	9 months	1 (14)	6 (3.8)	30	833 m (450–1,350)	36 ha (n = 1)	Srikosamatara, 1984
Hylobates syndactylus	Ulu Sempan, Malaysia	14 months[4]	1 (3)	4	6	778 m (485–1,390)	14.7 ha (n = 1)	Chivers, 1974
Hylobates syndactylus	Kuala Lompat, Malaysia	14 months[4]	1	5	5	969 m (320–2,860)	32.4 ha (n = 1)	Chivers, 1974
Hylobates syndactylus	Kuala Lompat, Malaysia	12 months[5]	1 (6)	3	5	738 m (200–1,700)	48 ha (n = 1)	Gittins and Raemaekers, 1980
Hylobates syndactylus	Ketambe, Sumatra, Indonesia	72 months	3 (7)	3.8	4	NA	NA	Palombit, 1992, 1994a

NA, not available.
[1] Number of groups surveyed.
[2] Majority of observations from a 10-month period.
[3] Extrapolated from data provided in reference.
[4] 173–190 days each site.
[5] Same study group (TS1) as Chivers, 1974.

TABLE 5. Taxonomy of the genus Hylobates

Genus	Subgenus	Species	Diploid chromosome no.
Hylobates	*Bunopithecus*	*hoolock*	38
	Hylobates	*agilis*	44
		klossi	
		lar	
		moloch	
		muelleri	
		pileatus	
	Nomascus	*concolor*	52
	Symphalangus	*syndactylus*	50

al., 1998; Palombit, 1994; Sommer and Reichard, 2000).

Gibbon home ranges vary from 5–500 hectares (ha), with most ranging between 10–40 ha (see Table 4). Between 70–95% of gibbons' home ranges are defended from conspecifics, with the majority of intergroup conflicts being resolved with little or no physical contact (Bartlett, 1999b; Brockelman and Srikosamatra, 1984; Chivers, 1984; Leighton, 1987). Areas with gibbon populations are frequently said to be saturated, with densities ranging from 5 to over 30 gibbons per square kilometer (see Table 4).

Gibbons exhibit species specific vocalizations referred to as "calls" (short vocalizations) and "songs" (longer vocalizations) (Haimoff, 1984). These vocalizations are sex-specific (except for *H. hoolock*) and are well-documented sonographically for most species. Males display solo songs, and females primarily exhibit their songs in a vocal duet with the male (*H. klossi* and possibly *H. moloch* may not perform duets; Haimoff, 1984; Kappeler, 1984). These duets are well-structured and are reported to play a critical role in gibbon intergroup interactions. Duets and male songs range from daily to once every 4–5 days, and the majority of intergroup conflicts are primarily vocal in nature (Brockelman and Srikosamatra, 1984; Leighton, 1987; Mitani, 1984). Duets may function as territorial announcements, intergroup spacing, pair-bond reinforcement, advertisement of paired status, and intragroup cohesion/coordination (Haimoff, 1984; Leighton, 1987).

PREVAILING VIEWS ON GIBBON SOCIAL ORGANIZATION

Below, I describe the hypotheses based on foraging (resource pressure), predation pressure, male investment strategies, and male mate guarding that have been invoked to explain gibbon group size, composition, and behavior. I then take a critical look at these hypotheses in light of the accumulated database for the hylobatids.

Foraging Strategies

Explanations of gibbon social organization (and monogamous mating pattern) revolve primarily around feeding ecology and aspects of gibbon behavior. They are derived from a larger body of avian and mammalian theoretical behavioral ecology, especially that regarding two-adult grouped and pair-bonded species (Table 3).

The *food competition or foraging hypothesis* (based on Horn, 1968; Wilson, 1975) suggests that group size is adjusted to the distribution and abundance of resources in time and space. Species relying on small, evenly distributed resources will best be able to utilize these resources if in small groups so as to minimize travel costs and to avoid high intragroup competition for food. Conversely, those specializing on large, unevenly distributed resources would benefit from larger groups both because of a relaxation of intragroup competition via a large food-patch size and the advantage that increased group size gives in intergroup competition for resources. Groups are expected to be as large as possible, given the normal size of feeding patches in order to defend those patches successfully.

While gibbons have been observed to feed on a wide range of foodstuffs, including high percentages of invertebrates and leaves, and lower percentages of bird eggs, flowers, shoots, and stems, they are primarily characterized as frugivores with an emphasis on figs (genus *Ficus*) (Leighton, 1987). Specifically, gibbons are said to focus on small-patch fruit sources that contain high-quality, inconspicuous fruits (Brockelman and Srikosamatra, 1984; Gittins, 1982). It has been argued that it is primarily this reliance on small patches as resources that has
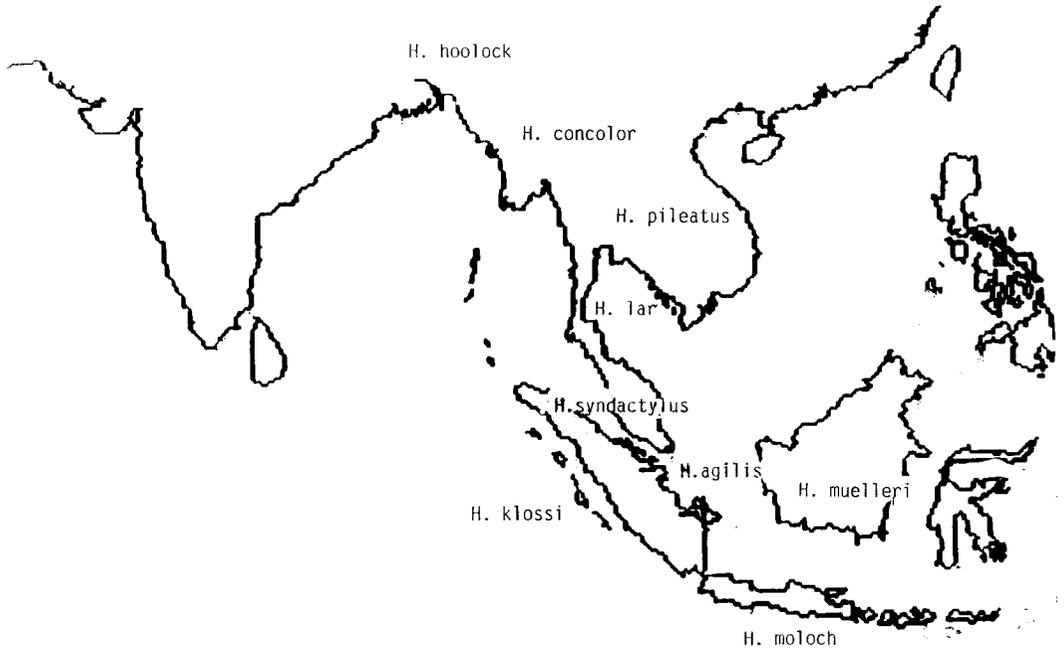
Fig. 1. Distribution of hylobatids.

molded the social organization of gibbons (Brockelman and Srikosamatra, 1984; Leighton, 1987). However, the range of dietary patterns reported for gibbons offers some challenges to this notion. While figs make up a significant portion of many gibbons' diets, Bartlett (1999a) suggests that most figs do not occur in small, evenly distributed patches. Rather, many figs occur in large trees that are quite common in some Southeast Asian forests (with one species occurring as much as 40 trees per hectare at Khao Yai, Thailand) and are available in high quantities year-round (Bartlett, 1999a; Leighton and Leighton, 1983). This suggests that fig exploitation may be a foraging strategy focused on an abundant food source distributed in large patches. Young leaves and invertebrates also make up significant portions of many gibbon species' diets. While both of these food resources may be distributed in small patches (small leaf flushes and single-species insect consumption), the strategies necessary for efficient exploitation of such foodstuffs can be quite distinct from the classic model of small fruit-patch foraging. For example, feeding

on leaves has higher processing costs and subsequent lower energetic return than feeding on Southeast Asian figs or other fruits (Waterman et al., 1988). Feeding on leaves also requires a different set of feeding patterns and digestion parameters (Waterman and Choo, 1981), which implies a foraging strategy different from feeding on figs or other fruits which are easier to process and digest but may involve higher intra- and interspecific competition. If gibbons are foraging on figs, leaves, and other food items, the foraging pressures affecting them do not appear to fit specifically into the parameters of the small, evenly distributed patch model presented above.

Brockleman and Srikosamatara (1984), Gittins and Raemaekers (1980), Wrangham (1979), and Wittenberger and Tilson (1980) focus on the reported small-patch foraging strategy of gibbons to explain hylobatid social organization. They argue for the hypothesis of *females as a limited or widely dispersed resource* (Rutberg, 1983; van Schaik and van Hooff, 1983; Wrangham, 1979, 1980). This hypothesis derives from hypotheses of Trivers (1972) regarding male

and female investment patterns. The basic tenets of this hypothesis are threefold. First, a given male cannot defend an area larger than an adult female's range, and this range is at least the area needed to satisfy the female's energetic requirements. Second, males cannot obtain more copulations under a roving male, or promiscuous, strategy than by opting for association with a single female (even if a male could copulate more frequently as a roving male, his actual reproductive success would be lower than within the two-adult group). Finally, a male could make it unviable for a female to resist his attempt to limit male group membership to one male, so that females remain with one male and do not copulate with others.

Brockleman and Srikosamatara (1984), Leighton (1987), and Tilson (1980) also invoke the *male defense against predators or defense against resource competition from conspecifics or others* hypothesis for gibbons (see Wittenberger and Tilson, 1980; van Schaik and Dunbar, 1990). This hypothesis assumes that male and female dietary requirements are significantly different, and that a reproductively active female is under dietary stress such that vigilance and related behaviors on her part would reduce her reproductive success by taking up feeding effort. Predation, under this model, is (or was until recently) a major threat to the species, so that male defense or vigilance is vital to successful reproduction. Alternatively, it may be that food competition with conspecifics, or other species, reduces a female's reproductive success unless a male (or both adults in the group) actively controls exclusive use of the group's resources. Finally, it is assumed that a change from a one-female to a two-female group would diminish the group's ability to defend its range from competitors, or that an increase in group size would make the females more susceptible to predation. These authors propose that the small-patch specialization of gibbons has favored small group size and territoriality (see Leighton, 1987). Even distribution and high quality of the small food patches would enable the female gibbons to subsist in relatively small home ranges and to be able to cover this range and effectively patrol it with the assistance of a male. Brockleman and Srikosamatara (1984), Leighton (1987), and Tilson (1980) also emphasize the role of female-female aggression and intrasexual aggression in the maintenance of the two-adult group. If there are high rates of female-female aggression due to resource competition and there is same-sex exclusion of maturing offspring by both sexes, one could see how this could act as a mechanism for the maintenance of the two-adult plus offspring group structure.

Predation pressure

The *predation pressure hypothesis* proposes that predation pushes primates towards gregariousness for improved predator detection, reduced risk of capture (selfish herd and dilution effects), and the potential for communal defense or defense by select group members (Dunbar, 1988; Isbell, 1994; Janson, 1992). This model suggests that when predation pressure is high, primates should live in larger groups. However, Tilson (1980) proposed an alternative form of this hypothesis where predation pressure favors very small groups that rely on predator avoidance via small group size and crypticity.

Sommer and Reichard (2000) suggest that predation pressure is a significant factor for the hylobatids. They report that two predation events have been recorded for gibbons (by python, Schneider, 1906 as cited in Sommer and Reichard, 2000; and leopard, Rabinowitz, 1989), and that gibbons respond to potential predators differently than they do to nonpredatory species.

Male investment strategies

The *assistance rearing offspring hypothesis* relates to group composition and is usually invoked for species that exhibit a high degree of paternal care. This hypothesis suggests that some species require a minimum of two adults (in the case of gibbons, an adult male and an adult female) to successfully raise offspring. This model has frequently been proposed as an explanation for the high occurrence of one-male/one-female and one-female/multimale groups in the callitrichids (Fuentes, 1999a; Kleiman, 1977; Rylands, 1993).

The *infanticide prevention hypothesis* explains gibbon social organization (Reichard and Sommer, 1997; Sommer and Reichard, 2000; van Schaik and Dunbar, 1990; van Schaik and Kappeler, 1997). This hypothesis rests on the assumption that infanticide is an important evolutionary force in primates and that it occurs in many or most taxa. Under this hypothesis, infanticide need not be common to affect social structure, for even at low levels the *risk* to both the female and the offspring's sire will be enough to select for appropriate counter strategies. It is assumed that adult females cannot defend their infants from infanticidal adult males and, therefore, need to form an alliance (pair bond) with an adult male to protect her offspring. A pair bond in this case should include a relatively high degree of paternity certainty on the part of the male. An important proposed correlate of this scenario is that behavioral elements observed in pair-bonded primates today may be the result of infanticidal pressure in the past (Sommer and Reichard, 2000; van Schaik and Dunbar, 1990). Van Schaik and Dunbar (1990) argue that gibbon males could potentially defend areas equal to several females' ranges (and thus have access to those females). Therefore, female distribution is not limiting males. They also argue against the *male defense against predators or defense against resource competition from conspecifics or others hypothesis*, citing evidence of range overlap and the lack of difference in range size between "widowed" female gibbons and pairs. Van Schaik and Dunbar (1990) propose that certain gibbon behaviors, such as males being the primary actors in intergroup conflicts, females not calling when solitary with young, and both males and females being wary of nongroup adults in their territory, reflect anti-infanticide adaptations.

Male mate guarding

Finally, Palombit (1999) proposed that gibbon social organization might be best explained via invoking the *mate-guarding hypothesis*. This hypothesis suggests that the pair bond is male-initiated and derived from a scenario in which by pair bonding with a female, any given adult male potentially maximizes his reproductive success (or at least minimizes the variance in his reproductive success). If females are widely distributed and food resources are patchy, a male can best maximize his reproductive chances by bonding with a female and attempting to insure maximal matings with her. This maximization can occur via deterring extrapair matings and/or restricting the female's ability to acquire information about extragroup males. If females seek occasional extrapair matings, males may also benefit by being "site-specific" to one female, and therefore, easily located by other females seeking extrapair copulations. Under this scenario males may not contribute any paternal care, in which case females are under what Gowaty (1996) terms "pair bondage," where it is less costly to tolerate a male's presence than to attempt to force him from her territory. Palombit (1999) suggests that given females as a limited resource (e.g., the small-patch feeding specialization), males should benefit by associating with one female and guarding her, while remaining site-specific and easy to locate (singing) for occasional matings with neighboring females.

All of the current explanations of hylobatid social organization rest, in part, on the basic assumptions that gibbons display small, cohesive family groups, monogamous mating, small-patch feeding, territoriality, and pair bonds among adults. These hypotheses attempt to explain why gibbons occur in small, discrete, territorial groups in which two adults form strong bonds and engage in monogamous mating. What if these traditional characterizations of gibbons are incomplete, or even incorrect?

I propose that the term "monogamy" and its related assumptions has constrained the investigations into hylobatid social organization (see Fuentes, 1999a). Recently accumulated data conflict with several generalized notions of how gibbons interact socially, how they feed and forage, and what types of groups they occur in.

NEWLY EMERGING PATTERNS IN HYLOBATID BEHAVIOR AND ECOLOGY

Over the last 20 years, primatologists have gathered a great deal of information on

the behavior and ecology of gibbons. Seven of the nine hylobatid species have been subject to field studies of greater than 12 continuous months in duration (see Table 4), and long-term studies on *Hylobates lar* and *Hylobates syndactylus* in Thailand and Indonesia have produced in-depth coverage of multiple groups within the same population. How does this information affect the current hypotheses put forward to explain gibbon social organization?

Foraging strategies

The concept of *females as a limited or widely dispersed resource* relies on female distribution and dietary patterns/resource stress.

Van Schaik and Dunbar (1990) tested the distribution of female gibbons as a limiting factor. They demonstrated, via an inverted Mitani-Rodman index, that female ranges do not limit a male gibbon and he would, potentially, be able to cover the range of more than one adult female.

Gibbons display remarkable diversity in dietary patterns. This conclusion can address issues of resource stresses on females. Fruits and flowers make up between 28% (*H. concolor*) and 72% (*H. klossi*) of gibbon diets, leaves from between 3% (*H. klossi*) and 72% (*H. concolor*), and insects from between 1% (*H. agilis*) and 28% (*H. syndactylus*) (Chivers, 1984; Palombit, 1997; Sheeran, 1993). There is also considerable evidence for variation within species across sites. For example, the percentage of leaves eaten by *H. concolor* in two studies were 72% and 43% (Sheeran, 1993). Whitten (1982b) reports almost no leaf eating by *H. klossi* in Siberut, Indonesia, whereas I noted leaves making up nearly 15% of the feeding observations of *H. klossi* in North Pagai, Indonesia (unpublished data). Given the time frame of most gibbon studies (∼1 year), there may be a wide set of seasonal variants (single or multiyear cycles) that are affecting these dietary patterns as well.

While gibbons are generally considered fruit specialists (Gittins and Raemaekers, 1980; Leighton, 1987), leaves and insects can make up significant portions of their diets. Palombit (1997) reports on dietary patterns including between 4–25% insects and 4–36% leaves for *H. lar* at Ketambe, Indonesia and Kuala Lompat, Malaysia, and 6–28% insects and 17–48% leaves for *H. syndactylus* at the same sites. Sheeran (1993) reports between 43–72% leaf use by *H. concolor*, and Whitten (1982b) notes that 24% of the *H. klossi* diet is made up of invertebrates. Most gibbon populations are reported to make heavy use of figs as a dietary component (Bartlett, 1999a,b; Palombit, 1997; Raemaekers, 1977). Figs that gibbons eat are generally found in large patches and are held to be a reliable year-round resource for primates in Southeast Asia (Bartlett, 1999a; Leighton and Leighton, 1983). The picture of gibbons as focusing on small, scarce food sources that are less conspicuous and attractive to other larger grouped organisms does not appear to take into account the diversity and focus of gibbon diet and feeding strategies reviewed here (see Bartlett, 1999a).

The varied nature of gibbon diets, within and across species, suggests that there is a greater potential flexibility in dietary patterns than previously considered. This flexibility may correlate with a diversity of feeding strategies relying on mixed patch sizes and various distribution patterns (see above, on foraging). It is possible that this diversity of dietary patterns and a related flexibility in female foraging are indications of less than severe limitations placed specifically on adult females due to the distribution of resources.

A third way to examine the *females as a limited or widely-dispersed resource hypothesis* is via an overview of group composition. If female distribution is limited by resource distribution, then greater than two adult groups should not occur (or be exceedingly rare) given the competition stress that would ensue unless the group experiences relatively relaxed resource competition pressure.

While the majority of gibbon groups observed contain only two adults, greater-than-two adult groups have been seen in 6 of the 9 species. There are no reports of greater-than-two adult groups for *Hylobates agilis*, *H. moloch*, and *H. muelleri*.

Hylobates concolor is observed in multiadult groups both on mainland Asia and in

an isolate population on Hainan Island in the South China Sea (Haimoff et al., 1986; Zhenhe et al., 1989; Sheeran, 1993). In the Ailao and Wuliang Mountains of Yunnan Province, China, gibbon groups have been reported consisting of up to 10 individuals in size, with 1 adult male and up to 4 adult females. This includes observations of at least one group in which both adult females had infants (Bleisch and Chen, 1991; Haimoff et al., 1986; Lan and Sheeran, 1995). Bleisch and Chen (1991) and Sheeran (1993) argue that the greater-than-two adult groups are rare for *H. concolor*, and may be due to habitat destruction or other ecological stress.

Zhenhe et al. (1989) reported on the demographics of the small population of *H. concolor* on the island of Hainan. While the total population numbered only 21 individuals in four groups, 2 of the 4 groups contained two adult females each. Of the total published reports of *H. concolor*, between 10–12 of the 36 groups surveyed (~27%) had greater than two adults (Bleisch and Chen, 1991; Haimoff et al., 1986; Lan and Sheeran, 1995; Sheeran, 1993). Of the 8 groups that have undergone longer-term observations, 2–4 had more than two adults (two groups had adult-sized, black individuals that were considered difficult to age; Sheeran, 1993; Zhenhe et al., 1989). Overall, these data suggest that approximately 25% or more of *H. concolor* groups have greater than two adults.

Hylobates hoolock is observed occurring in both greater-than-two adult bisexual groups and in all male groups. Siddiqi (1986) reported two adult males and a female in a group in Sylhet district, Bangladesh, and Ahsan (1995) reported two adult females and a male in a group at the same site. Mukherjee et al. (1991–1992) reported an all-male group of five adult males at Arunchal Pradesh in northeast India. Approximately 12% of the 34 *H. hoolock* groups that have been surveyed had more than two adults (Ahsan, 1995; Choudhury, 1990; Mukherjee et al., 1991–1992; Siddiqi, 1986; Tilson, 1979).

Hylobates lar is one of the two best-studied gibbon species. Carpenter (1940) reported on 21 bisexual groups in Thailand, two groups having two adult males, one group having two adult females, and two groups having two "young adults" in addition to the two "adults." Unless these two "young adults" were twins or are the result of severely delayed dispersal, it is unlikely, given a 2.5–5-year interbirth interval, that both of these adult-sized animals were similar aged subadults. Carpenter (1940) also reported collecting other groups, including one with two adult males and one female, and another with one male and three fully adult females. Sommer and Reichard (2000) reported 3 of 13 groups at Mo Singto, Khao Yai, Thailand having two adult males and one female. Ellefson (1974) also reported large groups with greater than two adult sized individuals per group. Esser et al. (1979) reported a range of adult composition in grouping patterns for semifree-ranging *H. lar*, with >29% of the groupings including more than two adults. Of the published reports of free-ranging *H. lar*, between 10–18% of groups are described as having more than two adults. (Brockleman et al., 1998; Carpenter, 1940; Ellefson, 1974; Gittins and Raemakers, 1980; Palombit, 1992; Reichard and Sommer, 1997).

In addition to the multiadult groups documented in *H. concolor*, *H. hoolock*, and *H. lar* in 1992, I observed nine *Hylobates klossi* (including five adult-sized individuals) in a cohesive association for approximately 4 months in North Pagai, Indonesia (unpublished data). Tenaza (1975) reported one group of *H. klossi* with two males, one of whom might have been an adult sized subadult, and one female in Siberut, Indonesia. Tilson (1980) also observed three groups with only one adult (an adult female) in Siberut. Brockelman and Srikosamatara (1984) observed a group of *Hylobates pileatus* that contained two adult females, each with young in Thailand, and Chivers (1974) reported one group of *Hylobates syndactylus* with two adult females.

In the six species observed in greater than two adult groups, at least 18% (26 of 144) of the groups surveyed/studied had more than two adults. Despite these reports of greater-than-two-adult groups, very few population-level surveys have been conducted. This hampers our ability to assess the percent-

TABLE 6. Percentage of greater-than-two-adult groups in gibbon species, based on citations in text

Species	% of total groups observed with more than two adult individuals
Hylobates agilis	No reports of greater-than-two-adult groups
H. concolor	25–27%
H. hoolock	12%
H. lar	10–18%
H. klossi	? (at least two greater-than-two-adult groups observed)
H. moloch	No reports of greater-than-two-adult groups
H. muelleri	No reports of greater-than-two-adult groups
H. pileatus	? (at least three greater-than-two-adult groups observed)
H. syndactylus	? (at least one greater-than-two-adult group observed)

age representation of greater-than-two-adult groups across the genus. However, this brief overview suggests that it is possible that at least 10% (or more) of gibbon groups may contain more than two adults (see Table 6).

In addition to same-species grouping, Brockelman and Srikosamatara (1984) reported naturally occurring mixed species (*H. lar* and *H. pileatus*) groups in Thailand. Interestingly, these groups are occasionally greater than two adult as well. At least two of these groups contain one adult male (either *H. lar* or *H. pileatus*) and one adult female of each of the two species. Fully fertile hybrid young have been produced, as have second-generation hybrids. Brockelman and Srikosamatara (1984) argued that these greater-than-two adult groups are due in part to the adult females of each species not recognizing each other as competitors or conspecifics. However, given that the male vocalizes, copulates, and interacts with both females, it is unlikely that this is the case. Alternatively, these cross-species associations are better seen as in line with the numerous observations of greater-than-two adult groups in *H. lar*.

The facts that 6 of the 9 species are observed in groups of more than two adults and that 63% of the greater-than-two-adult groups include two adult females suggest that the increase from one to two females may not cause significant stress on energy acquisition. That in at least three greater-than-two-adult groups both adult females have young infants further supports this assertion. However, a fuller range of data on reproductive rates and patterns in wild populations must be compiled to accurately assess the energetic constraints on female gibbons. While possibly not limiting the number of females to one, resource distribution may still act to limit overall group size in gibbons (as average group size is fairly consistent across all species; see Table 4). This suggests that within a certain group size, the actual number of adults may not be a limiting factor. Therefore, it seems unlikely that females are a *limited or overdispersed resource* across all hylobatids.

A correlate to the argument for dispersed/limited females is the notion of female-female aggression and expulsion of same-sex subadults by adults. This is proposed as a proximate maintenance mechanism for gibbon two-adult groups. The presence of multifemale groups presents an argument against the universality of hylobatid female-female aggression. If some of these greater-than-two-adult groups are the result of subadults remaining in their natal group, then the ubiquity of same-sex subadult expulsion is also called into question. Additionally, given the relative frequency of extrapair copulations (see below) and the variable duration of group membership, it is far from clear what the genetic relationship is between adult females (if more than one) and between adults and young within a group (at least for *H. lar* and *H. syndactylus*; see below). The pattern of short dispersal distance (see below) and observations of groups assisting subadults in establishing neighboring ranges also make it difficult to know the social and genetic relationships between females in nearby groups.

A fourth assessment of females as a *limited or overdispersed resource* in gibbons is via a comparative approach. If female gibbons are specifically resource-stressed, one would expect some behavioral indications. Given that male and female hylobatids are

monomorphic in size, one would expect a form of female dominance so that the female has guaranteed access, or at least first access, to favored food sources. We see just such a situation in the lemurs, *Lemur catta* and *Indri indri* (Pollock, 1979; Powzyk, 1997; Sauther et al., 1999). Interestingly, the indri (*I. indri*) occur in two-adult groups, engage in joint vocal displays, and have been described as analogous to the hylobatids. However, there are no reports of greater-than-two-adult groups, extrapair copulation, or affiliative behavior between groups for the indri (N = 5 groups studied; Pollock, 1977; Powzyk, 1997). Indri females are dominant to males and display quantitatively different feeding patterns from them (Pollock, 1977; Powzyk, 1997).

The lack of female dominance within a gibbon group and frequent reports of groups larger than five individuals suggest that small group size in the gibbons may not be best explained by describing adult females as limited by strict resource stress. The variability in gibbon diets also argues for a degree of flexibility in the diet and against a strict focus on small-patch food sources. Without a greater body of data concerning specific dietary/foraging differences between males and females, we cannot fully test the hypothesis that single adult females are what limit the size of gibbon groups. However, the data reviewed here do not appear to support the hypothesis that gibbon females are a limited or overdispersed resource.

Given defense of core areas and a majority of the home range by most gibbon groups, it is likely that some form of resource defense by group members is characteristic of the hylobatids. Therefore, the *male defense against predators or defense against resource competition from conspecifics or others hypothesis* is a possible factor in gibbon grouping patterns. All gibbon species are reported to engage in intergroup conflict. These conflicts are reported as rare in most species and range from primarily vocal exchanges to occasional physical aggression and wounding (Brockelman et al., 1998; Brockelman and Srikosamatara, 1984; Chivers, 1974, 1984; Kappeler, 1984; Leighton, 1987; Palombit, 1992; Sheeran, 1993;

Whitten, 1980). While gibbons appear to compete with other gibbon groups, long-term research on *H. lar* and *H. syndactylus* and briefer observations of *H. klossi* suggest that some groups act affiliatively with one another.

Carpenter (1940) noted up to three groups of lar gibbons directing cooperative displays at him and reported that groups displayed characteristics of having a set of intergroup dominance relationships. Reichard and Sommer (1997) and Brockleman et al. (1998) reported a wide range of affiliative behavior between some *H. lar* groups at Khao Yai. This behavior, ranging from mutual feeding associations to play and prosocial contact, accounted for approximately 35% of intergroup encounters observed (Reichard and Sommer, 1997). Palombit (1992) reported mutual tolerance and cofeeding by *H. lar* groups at Ketambe in Sumatra. Palombit (1992) also observed tolerance of cofeeding and general proximity between *H. syndactylus* groups at Ketambe. I observed an affiliative association between two *H. klossi* groups which lasted for approximately 4 months on North Pagai, Indonesia, in 1992. Tenaza (1975) observed a young adult female *H. klossi* move between associating with a solitary male and her group in the same range over the course of many months without aggressive interactions between the group and the male.

Reports of cofeeding and affiliation between groups indicate that not all resources are equally contested, nor are all groups necessarily seen as potential competitors. Further research into the specifics of exactly what gibbons are defending when they exhibit range defense will be vital to addressing the role of male defense.

It is also relevant that both adults and other group members participate in the most common form of defense: singing. While dueting is considered typical of the gibbons and a critical component of their pair-bonding, territoriality, and intergroup spacing (Chivers, 1974; Leighton, 1987; Mitani, 1985), many species exhibit a range of variability in this behavior (Colinshaw, 1992; Haraway and Maples, 1998; Sheeran, 1993). In *H. klossi* and *H. moloch* not all adult pairs duet (Colinshaw, 1992), and it is

debated whether *H. klossi* duet at all (Whitten, 1982). Typical song-bout duration ranges from 12 min in *H. concolor* to over 30 min in *H. klossi*, and species singing rates range from 0.28 (*H. syndactylus*) to 1.9 (*H. agilis*) songs per day (Gittins, 1984; Sheeran, 1993). Mitani (1984) argues that in *H. muelleri*, duets serve to mediate space between groups, and Colinshaw (1992) suggests that gibbon females sing as territorial defense and that duets reduce the cost of territorial conflict by advertising the coalitionary support of the adult males in potential intergroup conflicts. Colinshaw (1992) and Geissman (1983) reported that females occasionally sing male songs. Colinshaw (1992), comparing a wide range of gibbon species, reported little evidence for duets or other vocalizations as serving a role in the reinforcement of the pair bond. Geismann (1999), using *H. syndactylus* as an example, argues that the duet does serve a pair-bond function, with coordination of the vocal patterns in the duet acting as reinforcement of the pair-bonding process. However, Geismann (1999) also notes that a three-way duet (trio?) arose when a pair was formed with a solitary male in an adjacent cage, and that groups of siamangs in adjacent enclosures coordinated their calls and songs to one another (a personal communication by Nichloas Malone reported a similar occurrence at the Bali Gibbon Sanctuary).

We need to continue investigations along the lines of the experimental manipulations/observations of gibbon vocalizations by Colinshaw (1992), Geismann (1999), and Mitani (1984), to explore whether it is a "male" that is necessary for defense. It is possible that aspects of defense are tied to a specific group size, composition, or other characteristics. Given the observations of groups with only one adult maintaining range size and use, females' ability to sing "male" song, and differential response and variability in intergroup vocal interactions, we must be careful in assigning the successful defense requirement to a single adult male.

Predation pressure

Gibbons are considered to be under little to no predation pressure (aside from human hunting; Carpenter, 1940; Ellefson, 1974; Leighton, 1987). Sommer and Reichard (2000), however, conclude that "gibbons face considerable predation risk." They base this assertion on the dispersed sleeping patterns of gibbons and reported discrimination by gibbons of potential predators vs. nonpredators at Khao Yai, Thailand. However, no long-term gibbon study reports predation events, or attempts, despite many potential predatory species present. Very high rates of infant survivorship (Brocklemen et al., 1998), extreme arboreality, large body size (for an arboreal mammal), and lack of consistent antipredator behavior across sites suggest that it is unwise to currently assign a significant role of predation in the evolution of gibbon social organization.

Male investment strategies

Aside from the siamang (*Hylobates syndactylus*), there are few reports of any infant caretaking by male gibbons. This suggests that the *assistance rearing offspring hypothesis* does not currently appear to play a role in the evolution of gibbon social organization.

No study of gibbons reports either observed, attempted, or inferred infant killing by unrelated adults. One infant killing by the putative father was observed in *Hylobates hoolock* (Alfred and Sati, 1991). Van Schaik and Dunbar (1990) suggest that current gibbon behavior reflects a counter-infanticide strategy; however, recent research suggests that their assumptions about calling patterns may be inaccurate (see Geismann, 1999; Palombit, 1999). Also, there is a wide set of intergroup interaction patterns and variable responses to solitary adults which argues against a strong set of infanticide avoidance behaviors in gibbons.

In particular, variability in sexual patterns impacts the feasibility of this hypothesis. Only two gibbon species, *H. lar* and *H. syndactylus*, have been the subject of long-term study, with multiple groups being observed simultaneously. In both of these species, a significant behavioral deviation from the expected monogamous mating pattern is observed. At Khao Yai, Thailand, Brockelman et al. (1998) and Reichard and Sommer (1997) reported a significant amount of cop-

ulation outside of the group (termed "extrapair copulation," or epc). At least 12% of observed copulations at this long-term study site were epc, with many occurring during the females' estrus period (Reichard, 1995; Reichard and Sommer, 1997). At Ketambe, Sumatra, Indonesia, Ryne Palombit's 5-year study of three *H. lar* and three *H. syndactylus* groups also demonstrated the occurrence of extrapair copulation. These epcs ranged from "secretive" associations between nongroup adults to overt copulation in the presence of multiple adults from both groups (Palombit, 1992, 1994; Reichard, 1995; Reichard and Sommer, 1997).

Given the paucity of long-term observation of multiple groups and the reality of epcs, the genetic relatedness of individual gibbons within a "group" may be variable. Rather than being "nuclear families," some members of gibbon groups may be genetically unrelated. Carpenter (1940), Chivers (1974), and Tilson (1980) noted a number of apparent instances of incest within gibbon groups. However, it is quite possible that this "incest" is actually mating between unrelated (or distantly related) individuals.

Brockelman et al. (1998) reported that in a survey of 64 groups at Khao Yai, Thailand, 33% contained young less than 2 years apart (well under the average interbirth interval for gibbons). Additionally, four of the main study groups were also characterized as non-nuclear families. Brockelman et al. (1998) suggest that this may be the normative pattern for gibbons (at least for *H. lar* at Khao Yai).

Dispersal patterns could also impact the infanticide hypothesis. For the gibbon species in which dispersal distance is known, or inferred, or where actual dispersal has been observed, a consistent trend emerges. Long-term observations at Khao Yai, Thailand, place the average dispersal distance for *H. lar* at 710 m (with a range of 300–1,400 m, N = 7, Brockelman et al., 1998). Observers of *H. klossi* (N = 9 dispersal events) and *H. syndactylus* (N = 5 dispersal events) reported dispersal to the neighboring area or territory (Chivers, 1974; Palombit, 1992, 1994; Tilson, 1980; Whitten, 1980). Only Leighton (1987) for *H. muelleri* reported

that subadults consistently left the area when dispersing. His overview for 47 dispersal events in five gibbon species has 53% of individuals dispersing to the neighboring territory, 15% leaving the study site, and 32% with unknown dispersal results. Observers also reported codispersal by two individuals within a group and subadults receiving assistance from a group to establish a territory adjacent to that group's territory (Chivers, 1974; Palombit, 1992; Tilson, 1980). The short dispersal distances by both sexes could result in a pattern of known individuals residing in all, or some, of the ranges surrounding a given group's home range.

Related to this variability in group structure are a few reports of male care of young. While *H. syndactylus* has been noted as exhibiting some paternal care, observations of *H. agilis*, *H. concolor*, and *H. lar* also suggest some role of potential care behavior by adult males (Brockelman et al., 1998; Carpenter, 1940; Reichard and Sommer, 1997; Zhenhe et al., 1989). This is especially interesting given that some young in a group may not be related to the adult male.

The potentially high degree of genetic variability within gibbon groups, the variable nature of group residency/tenure, and the lack of evidence that infanticide occurs in gibbons suggest that the infanticide hypothesis is not supported for gibbons.

Male mate guarding

Palombit (1996, 1999) bases his *mate-guarding hypothesis* on the male bias in initiation and maintenance of adult-pair proximity in *H. lar* and *H. syndactylus* at Ketambe. However, he reported significant differences in the behavior of male *H. lar* and *H. syndactylus*, which he attributes to greater intragroup feeding competition in *H. lar* and paternal care in *H. syndactylus*. It is possible that intra-adult behavior is quite variable across gibbon species, and more data are required before we can assess the relationship between male behavior and a mate guarding strategy. For example, there is variation in sleeping patterns across species, with adult *H. klossi* spending very few nights in the same tree, adult *H. lar* spending approximately 40% of nights

together, and *H. syndactylus* spending nearly 90% of nights in the same sleeping tree (Palombit, 1992, 1994; Whitten, 1980). Spatial proximity also varies across these three species, with *H. syndactylus* adults spending from 9–23%, *H. lar* adults spending 4–8%, and *H. klossi* adults spending <2% of daytime activity in close proximity, grooming, or sitting in contact with each other (Palombit, 1992, 1994; Whitten, 1980). Reports of male infant care in *H. lar* (and other species; see above) and a wide range of dietary patterns within gibbon species also call into question some of the assertions regarding the benefits and patterns reflected in a mate-guarding strategy as proposed by Palombit (1992, 1994). This model is also based on the assumption of female distribution patterns and small-patch foraging as a basal strategy in gibbons (see *females as a limited or widely dispersed resource*, above). This model, as proposed by Palombit (1992, 1994), does not include any benefits for females and, in fact, implies "pair bondage" wherein the female tolerates the male's association, as it may be less costly to tolerate him than to drive him away. Again, the occurrence of greater-than-two-adult groups (especially two male groups) in many gibbon species poses a problem for this hypothesis. Accurate assessments of this hypothesis may well rest upon a focus on singing, grooming, and copulatory patterns within these greater-than-two-adult groups.

Where to now?

Despite the abundance of studies reviewed here, we are still in the data collection stage in our efforts to understand hylobatid social organization. This implies that we must take extreme care in postulating a priori explanations for their social organization. There are a number of critical areas where future studies will assist our endeavors. Genetic examination of hylobatid populations (underway at the Khao Yai site; Brockelman et al., 1998), long-term research on species aside from *Hylobates lar*, an emphasis on multigroup observation in gibbon field studies, and a continued focus on intergroup and intragroup behavior will broaden our basis for comparative analysis.

Continued study of dietary patterns, specific studies on dispersal patterns, and comparisons of the same species in different habitats/sites will also add substantially to our understanding of gibbon ecology (Brockelman et al., 1998; Reichard and Sommer, 1997).

NEW IDEAS ON HYLOBATID SOCIAL ORGANIZATION

In conclusion the lessons from our study are several: that gibbon group structure is more variable and less easily characterized than previously thought; that gibbon social development and mating opportunities are highly variable individually; and that intragroup behavior cannot be understood separately from a thorough study of intergroup interactions and changes.

—Brockelman et al. (1998, p. 338)

As early as the field studies of Carpenter (1940) and Ellefson (1974), and as recently as the overviews of Brockelman and Srikosamatara (1984) and Leighton (1987), gibbon researchers have been cautious in their assertions about gibbon social organization. We now have sufficient data to warrant not only caution, but an actual reassessment of how gibbons live and interact. We cannot best describe the hylobatids as living exclusively in nuclear family groups, engaging in strict territoriality, relying on a small-patch foraging strategy, or exhibiting only monogamous mating.

By shifting part of our focus from the gibbon "group" of a few adults and 0–4 young to include a broader multigroup or population level perspective, we may be better able to model gibbon societies (see Brockleman et al., 1998; Reichard and Sommer, 1997; Sommer and Reichard, 2000). If a majority, or even a significant percentage, of gibbon groups are not "nuclear families," and there is a significant rate of movement by individuals across groups and home ranges, then a long-term or broad-based view of a gibbon population may potentially reflect a form of supragroup organization.

If, as Brockelman et al. (1998) put it, "intragroup behavior cannot be understood separately from a thorough study of intergroup interactions and changes," then a beneficial mode of investigation into gibbon behavior could be to focus on intergroup dynamics at the population, or subunit of the

population, level. This approach was probably first, and most effectively, utilized by Kummer (1968) in his descriptions of the four levels of hamadryas baboon (*Papio hamadryas*) social organization. Izawa (1976, 1978) also promoted an analogous process of investigating intergroup dynamics and regional populations as a key to understanding the flexible social organization of the genus *Saguinus*.

It is readily apparent from the preceding review that the scope of interindividual interactions for gibbons includes individuals from multiple "groups" or clusters. While many individuals may spend a significant portion of their lives in two-adult clusters, they might also live as solitaries, in greater-than-two-adult clusters, and move among these clusters. It is possible then that hylobatid social organization could involve all of these patterns of interactions. I propose that the hylobatid social organization can be studied at the level of the population, or subsets of the population, referred to as *variable communities*.

A variable community of hylobatids can be defined as a set of relatively cohesive bisexual clusters averaging 3–5 individuals (adults and young) that occupy neighboring and somewhat overlapping ranges and habitually interact with each other. The composition of these clusters can be variable both temporally and individually, with some showing high cohesion and consistent composition and others showing low cohesion and highly variable composition. Relationships between the various clusters within a community may depend on their history of individual exchange, familiarity, range-use overlap, frequency of interaction, and age/sex composition.

These clusters are what we traditionally refer to as gibbon groups. However, the term "group" implies a discrete unit that is the main arena of social interaction for individuals within it. This does not appear to adequately describe the range of hylobatid social interaction patterns (nor does it always describe the main or only arena for mating and social interaction for some other primate species, e.g., Chism, 1999; Cords, 1987).

Investigating the evolution of hylobatid social organization

When investigating the evolution of any type of social organization, we need to remember that social organization is an emergent property, and not a distinct entity which itself is under selective, or other, evolutionary pressures (Allen and Starr, 1982; Hinde, 1976; Ray, 1999). We need to examine the sets of interindividual and intercluster interaction patterns in order to assess the possible evolutionary pathways that could have resulted in the current social organization. The assumption that all gibbon adults form the same strong, mutual, adaptive heterosexual pair bond and that this relationship forms the basis of gibbon social organization has not been adequately supported with data from field studies (see above). Rather, the current data suggest that there could be significant interspecific and interindividual variability in adult, within cluster, heterosexual association patterns (Brockelman et al., 1998; Palombit, 1992, 1994, 1996; Reichard and Sommer, 1997; Sheeran, 1993; Sommer and Reichard, 2000). Current gibbon patterns might not be exclusively "endpoints" of evolutionary processes. We may be observing a shifting social organization in the hylobatids. Instead of gibbons "having evolved" monogamy, family groups, and pair bonds, we can rephrase our investigations to examine gibbons as evolving organisms rather than perfectly adapted solutions to environmental challenges.

Recent evolutionary change in the hylobatids?

The variable genetic structure of the genus *Hylobates* suggests a recent diversification of species. The majority of species are allopatrically distributed, and those that share sympatric distribution also engage in some degree of hybridization in the wild (Brockelman and Gittins, 1984). There are also reported hybridization events in captive gibbons, even across different diploid number subgenera (Shafer et al., 1984). The late Miocene fossil *Laccopithecus*, from the Lufeng site in China, may represent a hylobatid ancestor; however, the assignment of
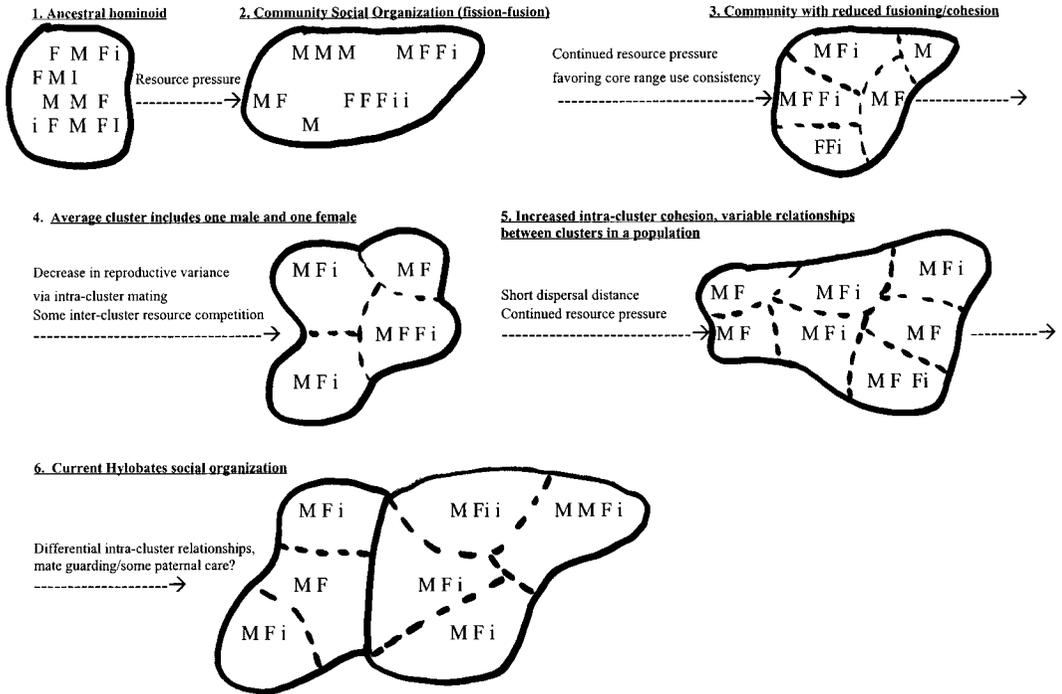
Fig. 2. Proposed hypothesis for gibbon "variable community." M, adult male; F, adult female; i, immature.

Laccopithecus as a fossil gibbon remains highly speculative (Fleagle, 1984, 1999). Rather, the majority of the hylobatid fossil record comes from mid-late Pleistocene fossils from Southeast Asia (Fleagle, 1984). Genetic analyses place the gibbon-other hominoid split to between 12–18 million years ago. However, there is a lack of consensus as to the relationships and timing of divergence between the four subgenera, which may be relatively recent (Pliocene or Pleistocene) (Cronin et al., 1984; Fleagle, 1999; Morales et al., 1999).

If a large or medium-sized multimale/ multifemale group were the ancestral pattern for the hylobatids, one could envision a gradual series of changes in which ecological and/or other pressures could facilitate the appearance of a fission-fusion, or community type, organization with variable cluster composition (Fig. 2). Once the majority of populations are distributed in a community-like social organization, local ecological pressures, intercluster conflict and affiliation patterns, and interindividual behavior patterns could potentially result in a

system such as the variable community social organization that I am proposing here. Given the differential environments and ecotypes in which gibbons occur, we would expect to see variation in the frequency, intensity, and quality of interindividual and intercluster interactions (as we do see across gibbon studies and species).

There are two major components to the scenario: phylogenetic aspects and current/ recent selective pressures. If hylobatid social organization has moved through the pattern illustrated in Figure 2, then phylogeny plays a significant role, i.e., multiadult bisexual grouping must have been the ancestral pattern for the hylobatids for this model to be feasible. One way in which this may be supported is if a generalized multimale/multifemale grouping pattern is ancestral for all hominoids.

Aspects of phylogeny

Pan troglodytes and *Pan paniscus* occur in multimale/multifemale groups described as "communities" (Goodall, 1986; Kano, 1992). These communities are divided into sub-

groups or "parties" that are variable in composition and size across time and space. Rarely, if ever, is the entire community in the same place at the same time. *Pan paniscus* parties are generally larger and more frequently bisexual than those of *Pan troglodytes* (Fruth et al., 1999). Intercommunity conflicts are reported to be less aggressive in *Pan paniscus* than in *Pan troglodytes* (Fruth et al., 1999). These differences are attributed to resource distribution patterns, especially the relative abundance of continuously available foodstuffs, i.e., terrestrial herbaceous vegetation, for *Pan paniscus* (Wrangham, 1986; Malenky and Wrangham, 1994). Parish (1994) suggests that *Pan paniscus* gregariousness may also be due in part to a tendency for females to form coalitionary relationships.

Gorillas (*Gorilla gorilla*) are frequently described as occurring in one male/multifemale groups; however, a number of reviews suggest that a significant number of gorilla groups are multimale (Doran and McNeilage, 1998; Goldsmith, 1996, 1999; Robbins, 1995; Stewart and Harcourt, 1987). Goldsmith (1996) documented multimale/multifemale groups that fissioned into smaller subgroups to feed and during times of resource stress. The gorilla's ability to effectively utilize herbaceous vegetation may allow for a relaxation of resource stress and facilitates a higher frequency of larger, bisexual groups (Goldsmith, 1996, 1999; Kuroda et al., 1996). Gorillas can be characterized as exhibiting a continuum of grouping from larger cohesive bisexual one-male or multimale groups to dispersed one-male or multimale subgroups that occasionally form larger groups (Doran and McNeilage, 1998).

All three of the African hominoids can be best described as occurring primarily in some variant of multimale/multifemale group that exhibits variable cohesion and group/subgroup size along a continuum. This variation is likely related to resource distribution and intra-individual sociality. The African hominoids exhibit a degree of arboreality, but also rely heavily on terrestrial locomotion and interaction patterns.

The largest Asian hominoid (*Pongo pygmaeus*, the orangutan), often described as solitary, is currently viewed as exhibiting a type of dispersed sociality, or individual-based fission-fusion grouping. Orangutan males have large, overlapping ranges that in turn overlap a number of females' ranges (Knott, 1999a,b; van Schaik, 1999). While frequently travelling and feeding alone (or with offspring), orangutans do aggregate in larger associations, with average party sizes being larger in Sumatra than in Borneo (van Schaik, 1999). While not exhibiting the degree of cohesion of the chimpanzee community or gorilla groups and subgroups, orangutans do exist in a social sphere where aggregations occur and adults interact with generally the same multiple individuals of both sexes on a regular basis (Knott, 1999a,b; van Schaik, 1999). The core component of the explanation for the reduced tendency to aggregate in orangutans again relies on resource distribution and composition *and* the extreme arboreality of this genus (Knott, 1999a,b; van Schaik, 1999).

The orangutan cannot be truly said to currently occur in a multimale/multifemale grouping pattern. However, orangutans do form large groups in captivity and at provisioned sites in Indonesia, although there is usually only one adult male present at a time. Given the overall similarities (fission-fusion) of the large-bodied hominoids in response to resource distribution, it is possible that the current orangutan grouping pattern is derived from a more gregarious multiadult group composition in the past.

It is *possible* that current hominoid social organization is derived from an ancestral state wherein our Miocene common ancestor occurred in multimale/multifemale groups that may have exhibited a tendency to fission and fusion relative to resource and social pressures. Because of the extreme sexual dimorphism in both gorillas and orangutans and its related implications regarding male-male competition and heterosexual dyadic interactions, we could see these hominoids as having deviated substantially from the common ancestor (assuming it was not as dimorphic). This leaves *Pan* and *Hylobates* as the two genera with little dimorphism (although more in *Pan* than in *Hylobates*). In both species, individuals are most likely to be found with five or

fewer conspecifics at any given time. *Hylobates* exhibits more cohesive, less variable, clusters than *Pan*. The two species of *Pan* (*paniscus* and *troglodytes*) vary in cluster size. Seasonality and food quality and distribution have been invoked to explain why *P. troglodytes* has smaller subgroups and fewer multifemale subgroups compared with *P. paniscus* (Fruth et al., 1999; Kano, 1992; Malenky and Wrangham, 1994; Stanford, 1998; Wrangham, 1986). Chimpanzees may also have access to a wider variety of resources as gibbons are 100% arboreal, whereas chimpanzees use both arboreal and terrestrial habitats. It is possible that aspects of food type, quality, and distribution in Southeast Asian forests are placing a different set of pressures on hominoid group size than in the forests of Africa (related discussions in Fuentes, 1994; van Schaik, 1999).

Current/recent selective pressures

It appears likely that some aspect related to the food competition or foraging hypothesis (Horn, 1968; Wilson, 1975) may be affecting cluster size in gibbons. Characteristics of evergreen Southeast Asian rain forests may play a role, given that the gibbon species in which most greater-than-two-adult groups have been reported are those with a broader distribution in seasonal forests (*H. concolor*, *H. hoolock*, and *H. lar*). Therefore, conditions favoring small clusters may be present for much, but not all, of the hylobatids' range. To further examine these pressures, we need to quantify the relationship between dietary diversity and composition, ranging patterns, and the frequency of greater-than-two-adult groups and multigroup cofeeding/tolerance/affiliation in the gibbons. Currently, we lack the appropriate long-term comparative data to assess the quantitative effect of resource distribution on the dietary patterns for most gibbon species.

The orangutan (*Pongo pygmaeus*), the gibbons (*Hylobates*), and the leaf-monkeys (*Presbytis*) are all arboreal, large-bodied, tropical forest-dwelling primates of Southeast Asia. The leaf-monkeys and gibbons are approximately the same size (6–12 kg), while the orangutan weighs up to 80 kg

(Fleagle, 1999; Rowe, 1996). The orangutan exists primarily in a dispersed social system in which the average cluster size is between 1–2 individuals (Knott, 1999a,b; van Schaik, 1999). Leaf-monkey (*Presbytis*) groups range from 2–22 individuals; however, the average size is between 8–9 (including at least two species in which average size is below five: *P. potenziani* and *P. aygula/comata*) (Davies and Oates, 1994; Fuentes, 1994; Kirkpatrick, 1999). While the orangutan and gibbons are generally described as focusing more on fruit than do the leaf-monkeys, many of the leaf-monkeys have diets that exceed 50% fruit (Kirkpatrick, 1999), and many gibbons have diets that exceed 50% leaves. If we compare these Asian primates with their African counterparts' group sizes (gorillas ~9–16 individuals, chimpanzees ~40 individuals, and colobus monkeys ~16 individuals), we see that the Asian forms occur in smaller sized groups (Goldsmith, 1999; Fruth et al., 1999; Kirkpatrick, 1999; Rowe, 1996). The differences in quality and distribution of food patches and types between Central African and Southeast Asian forests may favor smaller group size in arboreal primates in the Southeast Asian primary rain forest habitats. It is possible that the dominance of the family *Dipterocarpaceae* and its chemical structure may play a role here (Fuentes, 1994; Waterman and Choo, 1981; Waterman et al., 1988; Whitmore, 1984). Structural and floristic characteristics of Southeast Asian forests may be impacting the distribution and quality of food resources. The variability in leaf flushes and mast fruiting events related to multiyear cycles may create a broad seasonality (Whitmore, 1984), which in turn impacts grouping patterns in large-bodied, strictly arboreal mammals. While this suggestion is hypothetical, it is testable. By comparing the quality (extraction/processing costs to nutritive return) and distribution (temporally and spatially) of primary foods for populations of African and Asian apes, we may be able to correlate them with group sizes, activity budgets, and ranging patterns (e.g., McGrew et al., 1996; Sussman, 2000).

If resource pressure did/does favor smaller clusters, then we would still need to

explain why a majority of gibbon clusters consist (at any one time) of one adult male and one adult female. If, ancestrally, mating was intercluster (polygamous) and well as intracluster (monogamous/polygamous), we could potentially see a reduced variance in reproductive success if individuals mated within their cluster. That is, by mating with the most readily available partner (the other adult(s) in your cluster), additional costs of searching for mating opportunities are avoided (energetic costs such as long distance movement, potential physical conflict with conspecifics in new areas, or rejected mating attempts). Intracluster mating may also reduce the potential reproductive variance caused by rejected mating attempts by increasing mating receptivity via frequent intracluster social interaction between adults. Over many generations the strategy of minimizing reproductive variance could potentially have an overall fitness advantage for males over strategies aimed at maximizing reproductive success by exploiting as many novel opportunities as possible (given a highly variable return rate on extracluster mating attempts). This scenario allows for the occurrence of extracluster mating as the remnant of an ancestral polygamous pattern (i.e., some mixed strategy mating patterns would still be apparent, and they are, e.g., Palombit 1992, 1995; Sommer and Reichard, 2000).

In this scenario, given sexual monomorphism and no clear intra-individual dominance pattern in gibbon groups, female choice could become a critical component in the gibbon mating pattern. Behaviors such as mate guarding and paternal care of young could be seen as male responses to female mating selectivity. Palombit (1995) noted more variance than expected in reproductive success in seven female gibbons (*H. lar* and *H. syndactylus*) over a 6-year period and suggested that this may be an indication of strong selective pressure for mate choice.

While the hypothesis proposed here is primarily a phylogenetic one and thus difficult to test, we are able to assess its ecological aspects. We can attempt to determine if there are measurable differences between food quality and distribution in the forests of Africa and the forests of Southeast Asia, and whether or not those differences correlate with grouping and ranging patterns in hominoids. We can also attempt to untangle the relationship between arboreality and group size in hominoids in general. Further long-term and survey assessment of gibbon populations will also assess the actual percentage of greater-than-two-adult groups and their distribution across the hylobatids' range.

Alternatively. . . .

A logical objection to the scenario I have presented above is that rather than seeing a change from multimale/multifemale community to small clusters in a variable community, we are simply seeing food affecting female distribution, which in turn affects male distribution. The variation we see in gibbons' grouping and behavior patterns would simply be due to the environmental variation throughout their range as it relates to a female's ability to control sufficient resources. Wrangham (1979) suggested that it is a female's ability to defend a range containing sufficient resources that has led to a one-male/one-female grouping pattern and monogamous mating in gibbons. The starting point of such an argument is that ancestrally, or optimally, hominoid females foraged alone (without other females; Wrangham, 1979). Given that all extant hominoids are group-living (or some variant of that, as in the dispersed sociality of the orangutan), it is unlikely that the earliest proconsulids and other protoapes lived primarily as solitaries and that all of their descendants evolved larger social groupings. However, 3 of the 4 nonhuman hominoids do primarily forage in small groups (*Hylobates*, *Pan*, and *Pongo*).

Wrangham (1979) argued that in high densities females should "defend the boundaries of their foraging areas from others provided the benefits of exclusive use outweigh the costs of defense" (p. 348). Wrangham (1979) suggested that female gibbons (siamang in his example) are the only hominoid females able to effectively cover their foraging area and should therefore defend it against other females. This system produces

a selective regime under which monogamy is the most beneficial mating system. This model is a variant on the *females as limited/overdispersed hypothesis*.

However, it is currently unclear just what gibbons are defending in their ranges. We do not know if the average cluster size of 3–5 reflects limits on group size or age/sex class composition, and why not all clusters are equally defended against. Also, gibbons are not exclusively monogamous maters and do occur in two adult female groups. In short, the data suggest that females are not necessarily the main, or only, limiting factor for male gibbons. Current gibbon social organization may reflect a more complex evolutionary history than females mapping to resources and males mapping to females, given varying food distributions and population densities. However, this basic model (Wrangham, 1979) remains a viable hypothesis.

The main point of this paper is an attempt to provide an overview of current data on gibbon societies so that we can proceed more effectively with our theoretical analyses. There remain a number of viable hypotheses, as neither this paper nor any current treatment of gibbon sociality has effectively resolved the issues surrounding the origin and maintenance of gibbon social organization. By continuing to collect long-term ecological and behavioral data, we will be able to more effectively test these various hypotheses.

CONCLUSIONS

Given our current data set, it is apparent that the hylobatids are not "monogamous" primates, although monogamy is a mating pattern that may characterize a number of individuals in a population at any given time. Gibbon "groups" are not necessarily nuclear family units, nor is their composition necessarily invariable or stable over time; nor are they best seen as discrete entities that are the only critical arena for interindividual interaction. Rather, gibbons can be seen as living in bisexual clusters consisting of 3–5 individuals on average, with approximately 10% or more of these clusters having more than two adult members. These clusters do not necessarily consist of a mating pair and their offspring. A number of factors may be currently influencing hylobatid social organization. Structural and floristic characteristics of Southeast Asian forests could impact the distribution and quality of food resources. This in turn may be exerting a general size limit for the majority of gibbon clusters. All gibbon clusters exhibit some form of range defense, but ranges are not defended from all neighboring clusters. Gibbon clusters within a population appear to have variable relationships with one another, with affiliative behavior making up as much as a third of all intercluster interactions. It remains unclear as to specifically what gibbon clusters are defending when they do defend their ranges (or portions thereof).

Of the hypotheses reviewed in this paper (see Table 3), the *food competition or foraging hypothesis* and a variant of the *defense against resource competition from conspecifics or others hypothesis* (without a male as the focal requirement) remain potential avenues of continued investigation into gibbon social organization. It is also possible that *mate-guarding* and *paternal care* may be strategies practiced by males in some species of gibbons. The *predation pressure*, *assistance rearing offspring*, *females as a limited or widely dispersed resource*, and *infanticide hypotheses* are not supported by the information reviewed here.

In addition to the established hypotheses for gibbon social organization, I propose that gibbons currently exist in variable communities that have arisen via ecological pressure and specific behavioral patterns from an ancestral multimale/multifemale grouping pattern. I suggest that hylobatid social organization be characterized as changing towards a stable small-grouped, two-adult pattern. A multimale/multifemale ancestral grouping pattern for hominoids and smaller group size in Asian hominoids as compared with African forms based on resource differences would offer tentative support to the *variable community hypothesis*. This hypothesis was prompted by data from long-term multigroup gibbon studies (Brockelman et al., 1998; Palombit, 1992) and other gibbon studies that revealed variability in grouping patterns, intergroup be-

havior, reproductive patterns, and dietary patterns, and by the recent rejection of monogamy as a type of invariable social organization (French and Schaffner, 1999; Fuentes, 1999a).

This review of the hylobatids suggests that behavioral flexibility and variability may be normal for this group of primates (or even for primates in general; see Fuentes, 1999b). Our models may need to be multifaceted and include variability and the possibility that we are seeing various stages of the effects of natural selection, gene flow, and genetic drift at any given time. Therefore, simple or single causal explanations for diverse and complex interindividual and intergroup behavior sets might only provide incomplete answers.

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