Chapter 17
The Social Organization and Mating System of Khao Yai White-Handed Gibbons: 1992–2006

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Introduction

Nonhuman primates are well known among mammals for having a highly social nature and for developing individualized, long-lasting, intimate social relationships (Haimoff and Gittins 1985; Cheney et al. 1986; Rendall et al. 1996; Boesch and Boesch-Achermann 2000; Zuberbühler and Byrne 2006). In both gregarious and semisolitary primates such as orangutans, social relationships are characterized by repeated interactions with the same partners both within and between groups (Singleton and van Schaik 2002; Robbins et al. 2005). It has been recognized (e.g., Dunbar 1998) that a complex social life and long-term individual-based partnerships may require specific cognitive capacities and has been a primary force for the evolution of large brains in primates.

Within the realm of primate social systems, a great diversity of social relationships can be seen across age-sex classes. One component of the social system, commonly denoted as the social organization, describes how groups are organized with respect to the size, sexual composition, and spatiotemporal cohesion of social groups (Kappeler and van Schaik 2002). Another component of the social system involves how sexual relationships are distributed in a community. Sexual relationships represent a specific subset of social contact confined to patterns of mating, which are commonly referred to as a species' mating system (Kappeler and van Schaik 2002). A natural link exists between the mating system and the social organization, because the number of adults present within a social group may influence the availability of potential mating partners (Cords 2000; Müller and Thalmann 2000; Schwab 2000; Kudo and Dunbar 2001; Zinner et al. 2003).

Pair living was once believed to be the same as monogamous mating and vice versa, because individuals living in social pairs were assumed to be "faithful" to one another at least for a breeding season, or in extreme cases for a lifetime (cf. Reichard 2003a). Behavioral and genetic studies of the past two decades,

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however, have shattered the static, simplistic monogamy concept and it has now become evident that pair-living and monogamous mating are not synonymous (Birkhead and Møller 1996, 1998). Transitions between pair-living and polyandrous grouping, as well as monogamous and polygamous mating strategies, can occur in response to environmental and social changes or because the use of multiple, diverse mating strategies maximizes the reproductive success of group members (Davies and Lundberg 1984; Goldizen 1987; Zabel and Taggart 1989; Whittingham et al. 1997; Zinner et al. 2003; Schülke 2005). Hence, mating relationships in pair-living species are best understood as a visible outcome of compromises between the sexes over mating, including flexible responses to changing socioecological conditions (Davies 1992).

Gibbons are Asian apes that have until recently always been portrayed as holistically monogamous, at least in textbooks (e.g., Jolly 1985; Relethford 1996; Boyd and Silk 1997). Differentiation between the social organization and the mating system appeared superfluous: researchers agree that female and male gibbons are commonly found in pairs, they are renowned for their continuous spatiotemporal proximity on coinciding home ranges, and pairs show a high degree of behavioral synchronization and pair-specific behaviors such as duet singing (Chivers 1974; Haimoff 1984a, b). Duetting has been interpreted as a reflection of a particular form of social relationship between a male and a female termed a pair-bond (Geissmann and Orgeldinger 2000). The notion of obligate monogamous pairs of adults with offspring as core social units of gibbon societies was ubiquitous in early field studies after Carpenter's (1940) landmark, although brief study of wild white-handed gibbons in Thailand (Chivers 1974; Ellefson 1974; Tenaza 1975; Tilson 1979; Gittins 1980; Srikosamatara 1980; Kappeler 1984; Mitani 1984; Srikosamatara 1984; Leighton 1987). These consistent reports of pair-living were interpreted as evidence of obligate sexual monogamy despite the paucity of detailed information on sexual behavior in early monographs (e.g., Chivers 1974; Ellefson 1974).

The harmonious nuclear family model of gibbon social organization (Kleiman 1981) met its first challenge when Haimoff and colleagues (1986; 1987) reported multifemale grouping in black-crested gibbons (*Nomascus concolor*) of the remote Wuliang and Ailao Mountains, Yunnan, People's Republic of China, implying a polygynous mating system; however, subsequent studies failed to confirm deviation from both pair-living and monogamous mating (Bleisch and Chen 1991; Sheeran 1993; but see Jiang et al. 1999). Around the same time, Srikosamatara and Brockelman (1987) also reported deviation from the pair-living pattern when they described a multifemale pileated gibbon group (*Hylobates pileatus*) at Khao Soi Dao, Thailand, in which two females carried nursing infants. When two months later one of the females and her offspring had disappeared, Srikosamatara and Brockelman (1987) concluded that they had witnessed an exceptional and instable case of familial polygyny. When deviation from the two-adult pair-living pattern was noticed in early gibbon studies (summarized in Fuentes 1999, 2000; Reichard 2003b) these observations were interpreted, for example, as rare exceptions after long periods of social stability (Chivers and Raemaekers 1980) or as unusual cases of mixed-species group compositions in small hybrid zones between closely related species caused by inadequate female song recognition (Brockelman and Gittins 1984). The possibility of behavioral plasticity – condition-dependent variation in individual mating strategies – and the implications for understanding gibbon reproductive strategies and cognition are only now being addressed.

The slow pace of progress in unraveling gibbon societies is understandable given several factors. Attendant to the inevitable difficulties of observing natural populations, research efforts are hampered by gibbons' small group sizes and slow life histories (Reichard and Barelli 2008), short field studies of few years, and small numbers of habituated individuals (e.g., Chivers 1974; Ellefson 1974; Ahsan 1995) surrounded by intolerant neighbors. All of these factors resulted in unavoidable weaknesses in the early fieldwork, which so persuasively framed gibbons as a prime primate example of strict territoriality and monogamy. The absence of large long-term field studies of gibbons, i.e., studies involving multiple groups and spanning several generations, hindered the discovery of behavioral flexibility and documentation of the full array of gibbon reproductive strategies, including between-group contacts, natal and secondary dispersal (but see Brockelman et al. 1998; Lappan 2007a, b), and non-pair grouping and non-monogamous mating patterns.

More recently, our understanding of the gibbon social and mating system was extended when the results of a 6-year study of three siamang (*Symphalangus syndactylus*) and three white-handed gibbon (*Hylobates lar*) groups in northern Sumatra, Indonesia, were published (Palombit 1992). Palombit (1994a) documented numerous group composition changes and described the first observations of extrapair copulations (EPCs; Palombit 1994b), i.e., sexual contacts between individuals who did not maintain a close spatiosocial pair bond. Despite frequent group composition changes (Palombit 1994a), however, no deviation from the two-adult pair-living pattern was noticed. Shortly thereafter, flexible sexual behavior was reported in white-handed gibbons (*Hylobates lar*) in Thailand's Khao Yai Mountains (Reichard 1995b).

Following rapid advances in studies of pair-living birds (cf. Black 1996; Bennett and Owens 2002), which provided powerful theoretical tools for understanding behavioral flexibility in pair-living species, conceptual progress has begun to penetrate the study of hylobatid social and mating behavior (Brockelman et al. 1998; Fuentes 2000, 2002; Reichard and Boesch 2003; Barelli et al. 2008). In a series of detailed reviews, Fuentes (1999, 2000, 2002) summarized the anecdotes of deviation from pair-living in so-called "monogamous primates." These reviews raised a much-needed awareness of the subtle differences between pair-bonding behavior, a two-adult group composition and a monogamous mating system. However, empirical data that describe and quantify the variability of gibbon social organization and mating strategies are still rare.

It is my aim in this chapter to fill this gap with data from the longest ongoing field study on gibbons to date, which has focused on the Khao Yai white-handed gibbon population. Demographic records for the oldest known individuals in this population span almost three decades: I have followed the fate of many individuals since October 1989, forming the basis for the analyses presented here. I investigate the links between a variable social organization and the mating system of Khao Yai gibbons with new demographic and behavioral data to evaluate behavioral flexibility in social grouping (social organization). I then take a closer look at sexual relationships and the mating system of Khao Yai gibbons. The chapter concludes with a discussion about the possible links between behavioral flexibility in social organization and mating, aspects of resource competition, and the evolution of gibbon cognitive evolution. Information on the genetic mating system of Khao Yai gibbons is not yet available.

The Flexible Social Organization of Khao Yai Gibbons

Anecdotal evidence of variation in the social organization of gibbon groups has accumulated in recent years for some populations (e.g., Brockelman et al. 1998; Fuentes 1999; Sommer and Reichard 2000; Reichard 2003b; Lappan 2007a,b). Based on a literature review, Fuentes (2000) hypothesized that 10% or more of gibbon social groups contain more than two unrelated adults. However, besides sporadic observations of non-pair-living groups, empirical data that will allow confirmation or rejection of Fuentes' (2000) estimate are not yet available.

Mo Singto – Klong E-Tau Study Site

Data on the Khao Yai white-handed gibbon social organization come from the Mo Singto – Klong E-Tau study site, Khao Yai National Park, Thailand (2,168 km^2; 101°22′ E, 14°26′ N; ~ 130 km NE of Bangkok; Fig. 17.1). Khao Yai National Park is part of the Dong Phayayen – Khao Yai Forest Complex (DPKY), which covers an area of 6,199 km^2 (Lynam et al. 2006) and has recently been designated a World Heritage site (UNESCO 2005). The Mo Singto – Klong E-Tau study site is a continuous forest area that covers approximately 8.5 km^2 of slightly hilly terrain (730–890 m above sea level) and is located in the central portion of the Khao Yai Mountains. Population density at the site is high, at ~4 groups and 15.9 individuals/km^2 (Fig. 17.1), but remains within the ranges of population densities reported from other field studies (Leighton 1987; Mitani 1990b; Borries et al. 2002; Bartlett 2007).

The Khao Yai Mountains are largely covered by seasonally wet evergreen forest (Kerby et al. 2000; Kitamura et al. 2004). The park experiences a distinct dry season (November–April) and a wet season (May–October) with an overall average precipitation of ~2700 mm (January 2001–December 2003).

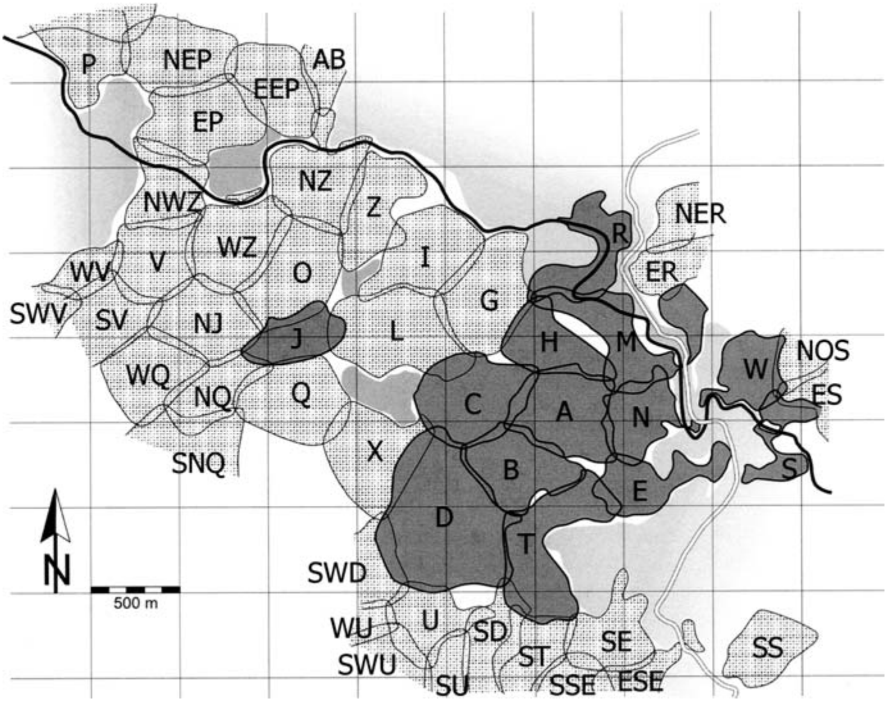


Fig. 17.1 Mo Singto – Klong E-Tau study site with home range outlines of habituated and neighboring study groups, Khao Yai National Park, Thailand. Thick, *solid line* = Lam Takhong river; thick, *open line* = N-S road traversing national park; *letters* = gibbon home range outlines; *dotted home ranges* = approximately known home range outlines; *fading areas* = grassland, patches of open canopy or low canopy regenerating forest along the river

Mixed Species Groups

Gibbon species are commonly allopatric and only few contact and natural hybridization zones between closely related species have been described (Brockelman and Gittins 1984). The Mun River and its tributary, the Takhong, mark the geographic distribution boundary of white-handed (*Hylobates lar*) and pileated gibbons (*H. pileatus*) in Northeast Thailand (Srikosamatara 1984). In the headwaters of the Takhong, around Haeow Suwat waterfall, in Khao Yai National Park, a contact zone exists where mixed-species trios have been described, i.e., a male–female pair and another adult of either species or a hybrid (Marshall et al. 1972, Brockelman and Srikosamatara 1984). The contact zone is narrow and populations only ~10 km away are again dominated by either white-handed or pileated gibbons (Brockelman and Gittins 1984).

The tip of the Mo Singto – Klong E-Tau study site closest to the contact zone is approximately 20–30 km away. In 1997, a single pileated gibbon female migrated into the study site and became resident on one particular home range. Over the years, this female has been involved in various partnerships with white-handed gibbon males and females (see Table 17.1). Because of the

Table 17.1 Frequencies of solitary individuals and social groups in Khao Yai, Thailand, white-handed gibbons

Census year$^{\#}$	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Mean ± SD
Solitary individuals																
females [N]	0	0	0	–	0	0	0	1	1	0	1	0	0	0	0	
males [N]	1	1	0	–	0	0	0	0	1	0	0	0	0	1	0	
[%]	7.1	6.3	0	–	0	0	0	3.8	8.3	0	3.4	0	0	6.3	0	2.5 ± 3.2
Groups																
pair-living [N]	12	14	10	–	12	12	13	20$^{\partial}$	19$^{\partial}$	31$^{\partial}$	23$^{\partial}$	10$^{\partial}$	10$^{\partial}$	9	9$^{\partial}$	
[%]	85.7	87.5	90.9	–	85.7	85.7	81.3	76.9	79.2	88.6	79.3	76.9	66.7	56.3	60.0	78.6 ± 10.7
multimale single-female [N]	1	1	1	–	2	1	1	4	2	3	5	3	5	5	5	
[%]	7.1	6.3	9.1	–	14.3	7.1	6.3	15.4	8.3	8.6	17.2	23.1	33.3	31.3	33.3	15.8 ± 10.4
multifemale single-male [N]	0	0	0	–	0	0	1	1	1	1	0	0	0	1$^{\partial}$	0	
[%]	0	0	0	–	0	0	6.3	3.8	4.2	2.9	0	0	0	6.3	0	1.7 ± 2.5
multimale multifemale [N]	0	0	0	–	0	1$^{\partial}$	1$^{\partial}$	0	0	0	0	0	0	0	0	
[%]	0	0	0	–	0	7.1	6.3	0	0	0	0	0	0	0	0	1.0 ± 2.4
Total units	14	16	11	–	14	14	16	26	24	35	29	13	15	16	15	

= data collected during last quarter of calendar year (Oct–Dec).

∂ = one group included the same pileated gibbon female (H. pileatus) across all years.

_ = no census conducted.

mixed-species status, I interpreted the groups in which this female was involved as exceptional (see below: Social Organizations In Khao Yai Gibbons). She was the only pileated gibbon individual in this sample, although beyond the immediate study site occasionally pileated or pileatus-lar-backcross females were heard singing.

Social Groups

The term “social group” is used to describe the social organization of group-living gibbons and I use “solitary individual” to refer to animals that appeared to be alone or “floating” (Cowlishaw 1996). Individuals were considered adult once they completed physical growth, which in this population does not occur before the age of 7–8 years in females and about 8 years in males (for age-class definitions see Reichard 2003b).

Data Collection

Part of the Mo Singto – Klong E-Tau gibbon population has been studied since the early 1980s (Treesucon 1984; Raemaekers and Raemaekers 1985; Whitington 1990), but behavioral observations and demographic records presented here are based on the observations collected by field assistants and myself between October 1989 and December 2006. In 1989, a single gibbon group was habituated (group A), but by the end of 2006 this number had grown to 14 (Fig. 17.1). Systematic annual censuses (Ross and Reeve 2003) were conducted from 1992 to 2006 and included 44 social groups over the years. Group compositions were irregularly tracked throughout those years, but identification and designation of social groups was confined to the census results collected during the last quarter of each calendar year, except 1995. Instead of a census in late 1995, a census was carried out in early February 1996 to detect composition changes, but those survey results were excluded from the data set. The majority of social groups were contacted repeatedly each year; the habituated study groups in particular were continuously monitored, because they were the focus of intense, systematic data collection for other purposes (Nettlebeck 1993; Neudenberger 1993; Reichard and Sommer 1997; Reichard 1998; Sommer and Reichard 2000; Chambers et al. 2004; Clarke et al. 2006; Fürtbauer 2006; Barelli et al. 2007; Savini et al. 2008).

All individuals encountered during census walks were assigned to one of two categories based on their solitary or group living status. Individuals were designated “solitary” if they were continuously without other gibbons. An individual in the company of other gibbons was considered a “member of a social group.” Members of social groups were usually easily identifiable, because they coordinated daily activities, frequently interacted with and stayed more or less continuously in spatial proximity with other individuals (e.g., remaining within view for most of the day). Cohesion is notably high in white-handed gibbons (Nettlebeck 1993; Neudenberger 1993; Reichard

1995a); only mature male offspring occasionally range further than 50 m from others for periods exceeding an hour (Fürtbauer 2006).

Individual Recognition

Individuals were recognized based on three traits: (1) Pelage color: white-handed gibbons at Khao Yai are asexually dichromatic. They are dark or buff, which was recognizable within the first week of life. (2) Shape, size, and "whiteness" of the white face ring, eyebrows, and white areas of the hands and feet; and (3) idiosyncratic markers (scars, stiff or missing fingers or toes, etc.). I distinguished a black (coded: black-dark) and a brown (coded: brown-dark) type of the dark color morph and a light (coded: light-buff) and cream-brown (coded: cream-buff) type of the buff morph to aid individual identification. The white circumfacial pelage marking is a reliable, individually recognizable feature in many hylobatid species including white-handed gibbons (Geissmann 2003).

Field Key to Identify Social Groups and Solitary Individuals

A hierarchical, three-step key was used to determine the composition of social groups and solitary individuals in the field (Fig. 17.2).

Step one: the number of adult individuals present was counted. (i) If an adult was encountered alone and neither joined nor was joined by members of a social group during the observation period, that individual was considered *solitary* (*n* = *7 individuals*). Contact times with solitary individuals were short (range: 10–55 min), because solitary individuals were shy and unhabituated except for one well-known young adult male who had dispersed from its natal group about a year prior to the time when he was found to be solitary. Unfamiliar solitary

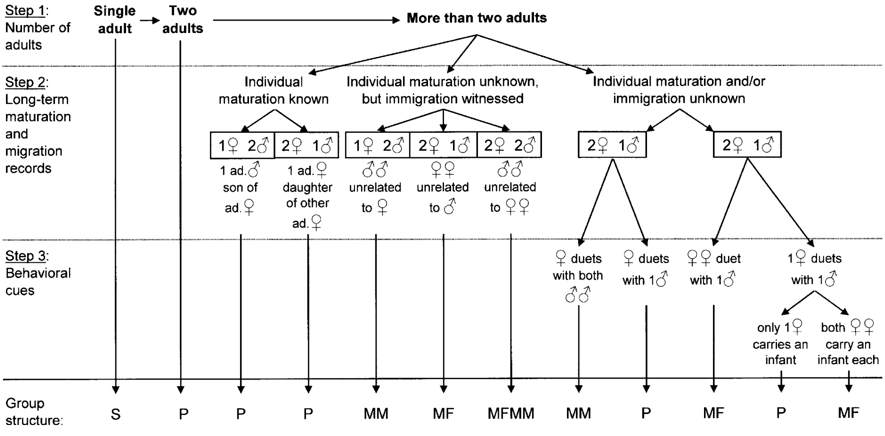


Fig. 17.2 Social organization identification key. ad. = adult; S = solitary; P = pair-living; MM = multimale; MF = multifemale; MFMM = multifemale-multimale

individuals all fled rapidly after having spotted a human observer and thus naturally limited observations could be made while hiding. Despite pursuit of fleeing solitary individuals, none was contacted a second time on the same day or later. (ii) If only two adults were counted as the social group, they were always considered *pair-living* ($n = 155$).

Step two: When more than two adults were counted ($n = 96$ social groups), long-term maturation and migration histories were used to differentiate groups with mature adult offspring (46% of groups) from groups with an additional, unrelated adult (54% of groups). Social histories are known from my own long-term monitoring of the population spanning more than 3200 h of direct observations spread across more than 500 days over 17 years (October 1989–December 2006). These data were complemented with published migration and maturation records of individuals in study groups A, B, and C (Treecuson and Raemaekers 1984; Treesucon 1984; Whitington 1990; Brockelman et al. 1998). (iii) Groups with three adults including a mature offspring were always identified as *pair-living*, based on the assumption that mature offspring were nonbreeders in their natal group and hence would not count as potential mates. In groups where social histories of all offspring were known, no copulation attempt with an offspring has ever been recorded. Hence, for groups with an adult offspring, I assumed that the offspring delayed dispersal, which has been documented for this population (Brockelman et al. 1998). Therefore, such a group functionally resembled a pair-living group. (iv) If more than two adults were present and migration – i.e., emigration or immigration – of an adult had been witnessed, social groups were considered *multimale, multifemale*, or *multimale multifemale*. The combination of social- and migration-history records suggested it was highly unlikely the immigrant was related to the opposite-sex breeding adult in his new group. Designation of social organization was independent of kin relationships between same-sex adults in groups, as I was primarily interested in the number of potential breeding partners within social groups. For example, a group with a (presumed) father–son pair was identified as multimale if the son's mother was replaced by a new female, because both males were potential breeding partners of the new female.

Step three: If more than two adults were present in a group, but individual social histories and migration patterns were unknown ($n = 10$ groups; five groups with two females; five groups with two males), social groups were categorized following behavioral cues. Group structure assignment in the absence of individual social histories or migration was conservative; groups were considered pair-living unless clear deviation from behavioral patterns consistently observed in pair-living social groups strongly suggested a different structure. By definition, this procedure can lead to overestimation of the proportion of pair-living, but not group-living, individuals. The following behavioral cues and procedures were used to identify deviation from patterns seen in pair-living groups: (1) In groups with two adult males, (a) if a female sang duets with both males, the group was classified as *multimale*, because long-term observations of habituated groups revealed that mature sons never sang duets with their mothers (unpublished data). (b) If instead, a female consistently sang duets with only one male, the group was assumed to be pair-living and one adult male was presumed to be the female's mature son. A common singing pattern in known multimale groups featured one male consistently and the other occasionally singing duets with the female. (2) In groups with two adult females, (c) a group was considered multifemale if both females alternated duet singing with a male or both carried a dependent infant. (d) The group was considered pair-living if only one female sang duets and only the same female carried an infant, in which case one female was assumed to be a retained adult daughter.

In social groups with more than two adults where individual social histories were known, an age-difference between same-sex adults was usually noticeable. However, age was not used as a variable in assigning social organization for two reasons: birth dates were unknown for many individuals, and visual age estimates in the absence of known birth dates were subjective.

Social Organizations in Khao Yai gibbons

Two hundred and fifty-one ($n = 251$) social groups and seven solitary individuals ($n = 7$) were recorded over 14 census years (1992–2006). Because gibbon groups at Khao Yai are territorial and spatially stable, most individuals were censused multiple times during consecutive years. In contrast, all solitary individuals were encountered only once. Thus, the sample comprised seven solitary individuals and 44 groups (Table 17.1). Three social groups ("K", "Y", and "WJ") dissolved after 1, 2, and 3 census years, respectively. Of the remaining social groups ($n = 41$), about one-third were censused only once, primarily during extensive census walks in 2001 and 2002. Nearly half (46.3%) were censused over at least 5 years, about one-third were censused over at least 10 years, and six groups (13.6%) were censused each year over the entire 14-year study period.

Solitary individuals of both sexes were infrequently encountered and constituted on average less than 3% of the communities' social groups and solitary individuals across years (Table 17.1). During 57% of census years no solitary individual was discovered. All solitary individuals were shy (average contact time <60 min) and, by definition, had no contact with other gibbons and neither engaged in intergroup encounters nor vocalized loudly. The only exception was one habituated, postdispersal young adult male, who was found singing a loud male solo song in an area of degraded, low-canopy forest bordering grassland, where no gibbons had been previously seen. Solitary animals seemed to lack a defined home range as inferred from single contacts even in areas walked frequently. They were encountered while quietly foraging in peripheral/overlapping areas between the adjacent home ranges of known social groups. All but the solo singing male immediately fled upon noticing a human observer.

The majority of social groups across census years were pair-living (average ± SD across years: 78.6 ± 10.7% of groups and solitary individuals; Table 17.1). However, more than two adults were found in 18.3% of groups ($n = 251$ groups; excluding solitary individuals). Most non-pair-living groups were multimale (average ± SD across years: 15.8 ± 10.4% of groups and solitary individuals, see Appendices 1, 2, 3, and 4), but maximum group size did not exceed six members. Multimale groups typically contained only two adult males except in one group where three adult males lived together with one adult female for several months (see Appendix 2). Other social arrangements were rare. For example, one-male multifemale groups were recorded only five times (average ± SD: 1.7 ± 2.5% of social groups and solitary individuals, see Appendix 3), and only one mixed-species multifemale multimale group was recorded; the same group was observed during two consecutive census years (average ± SD: 1.0 ± 2.4% of groups and solitary individuals, see Appendix 4).

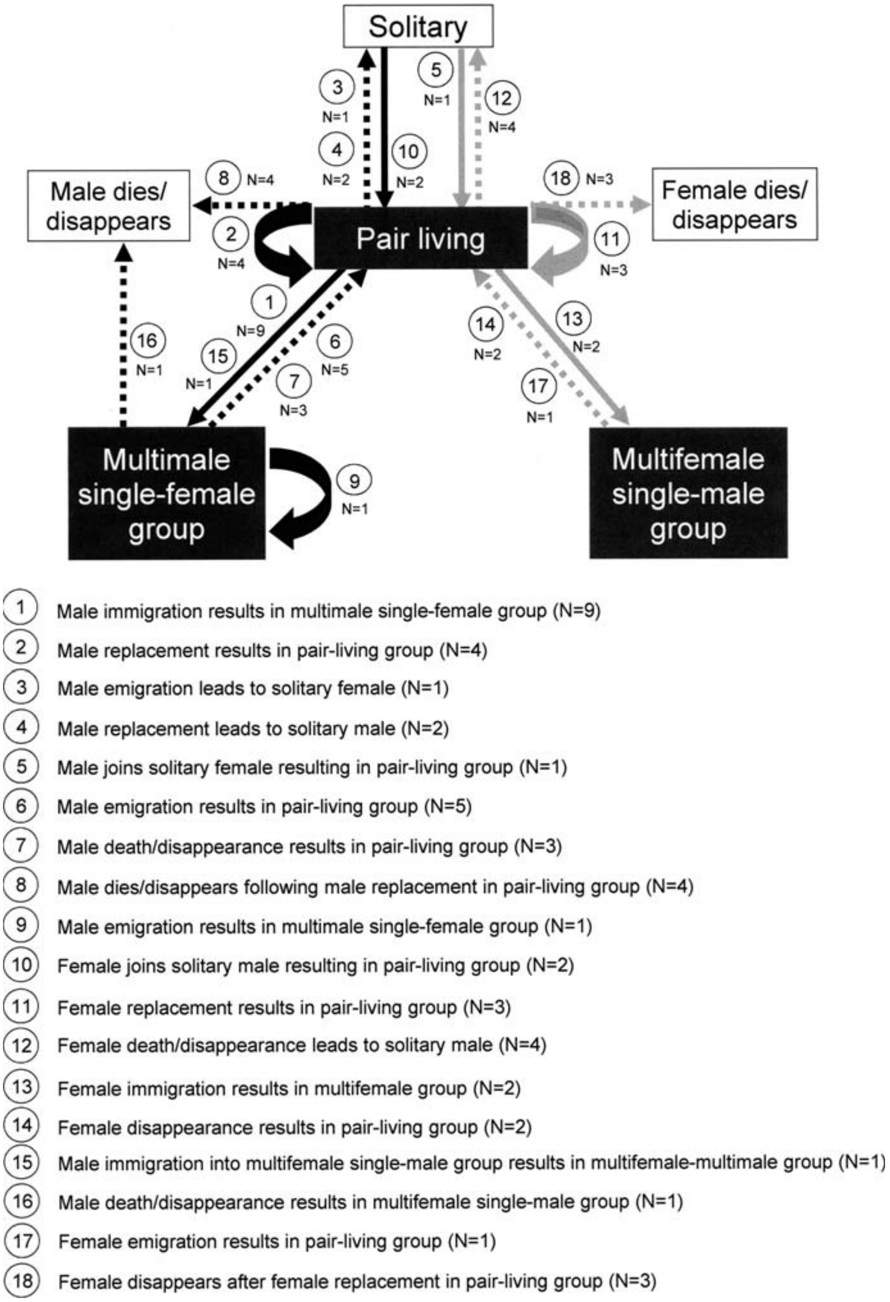
Pair-living and multimale grouping seemed to be alternative strategies in the Khao Yai population, because (1) only pairs and multimale groups were frequent (i.e., > 5% of groups) and consistently present throughout the entire 14-year study period. In contrast, other group types showed considerable inter-annual variation and were absent during most census years. (2) Group formation and dissolution was witnessed only for pairs and multimale groups, except for the formation of the exceptional mixed-species multimale multifemale group (Fig. 17.3). (3) Only pairs and multimale groups were stable over time and lasted several years. The longest known multimale group existed for 12 years; the longest known pair-living groups existed for 14 years. In contrast, the longest known multifemale group existed for about two years.

The Variable Mating System of Khao Yai Gibbons

Assessment of sexual activities of Khao Yai gibbons was limited to a subset of individuals included in annual censuses, because mating was infrequent and largely unpredictable. Documentation of sexual interactions required observing habituated individuals to avoid bias against observations of non-monogamous mating, as the chance to witness non-monogamous mating behavior in a dyad where only one member is habituated is negligible.

Sexual Behavior Data Collection

Data on sexual behavior presented here come from the Khao Yai long-term database accumulated by field assistants, students, and me, entered on daily observation check-sheets since October 1989. Mating behavior was recorded following standard instantaneous, continuous, or *ad libitum* sampling methods (Martin and Bateson 1993).



① Male immigration results in multimale single-female group (N=9)
② Male replacement results in pair-living group (N=4)
③ Male emigration leads to solitary female (N=1)
④ Male replacement leads to solitary male (N=2)
⑤ Male joins solitary female resulting in pair-living group (N=1)
⑥ Male emigration results in pair-living group (N=5)
⑦ Male death/disappearance results in pair-living group (N=3)
⑧ Male dies/disappears following male replacement in pair-living group (N=4)
⑨ Male emigration results in multimale single-female group (N=1)
⑩ Female joins solitary male resulting in pair-living group (N=2)
⑪ Female replacement results in pair-living group (N=3)
⑫ Female death/disappearance leads to solitary male (N=4)
⑬ Female immigration results in multifemale group (N=2)
⑭ Female disappearance results in pair-living group (N=2)
⑮ Male immigration into multifemale single-male group results in multifemale-multimale group (N=1)
⑯ Male death/disappearance results in multifemale single-male group (N=1)
⑰ Female emigration results in pair-living group (N=1)
⑱ Female disappears after female replacement in pair-living group (N=3)

Fig. 17.3 Membership transitions in social groups in white-handed gibbons. *Light gray* = change involving female; *black line* = change involving male; *broken line* = subtraction; *solid line* = addition; *bent arrow* = change in individual membership without change in social organization

Identification of mating strategies follows common classifications. Males seen to mate with only one female partner were categorized as sexually *monogamous*; males who mated with multiple females were considered sexually *polygynous*. Females seen to mate with a single male mating partner were identified as sexually *monandrous* and those with multiple partners as sexually *polyandrous*.

Individual contribution to the data set of sexual activities was heterogeneous, because adult individuals spent between <1 month and 14 years continuously in the population. This extreme individual variation occurred because individuals matured or disappeared at different times during the long data collection period. A detailed description of individual contributions to the overall observation period and social histories in relation to sexual activity is omitted, because high interindividual variation with regard to time of maturation or continuous presence in the study population would have required lengthy case-descriptions of many individuals. Varying individual contribution to the data set did not bias my analyses because I was primarily interested in gross patterns of mating strategies.

The Data Set of Adult, Sexually Active Gibbons in the Population

Between 1992 and 2006, fifty-four adults ($n = 25$ females, $n = 29$ males) were resident in fourteen habituated focal groups (A, B, C, D, E, H, J, M, N, NOS, R, S, T, and W). Thirty-three sub adults reached adulthood during the study ($n = 15$ females, $n = 18$ males). Of these matured subadults, seven males and six females disappeared with unknown fate after their natal dispersal, as did one female upon reaching maturity, which coincided with her secondary dispersal. These individuals were omitted from analyses, although they were technically adults in the population. Of the remaining matured subadults ($n = 8$ females, $n = 11$ males), two males and one female delayed dispersal, whereas nine males and five females remained in the study population after successful dispersal. Two females that reached adulthood were seen copulating for the first time with immigrant males prior to natal dispersal and were included in the analyses despite their dispersal/disappearance with unknown fate shortly thereafter.

In summary, data on sexual activities originate from 17 females ($n = 17$) and 20 males ($n = 20$) that were adult at the onset of observations and eight females ($n = 8$) and nine males ($n = 9$) that became adults over the course of data collection. The following analyses treat all 25 adult females and 29 adult males equally, independent of their maturation history.

No mating behavior was recorded for 12 females (48.0%; $n = 25$) and 10 males (34.5%; $n = 29$ males; Tables 17.2 and 17.3). Of this group, it is unlikely that sexual strategies were adequately documented for six females and five males, because (a) four individuals remained in their natal groups (three males, one female); (b) one male and one female were only very briefly seen after dispersal before their disappearance; (c) one female and one male disappeared shortly after the beginning of data collection, and (d) three females

Table 17.2 Sexual strategies of wild white-handed gibbon females, Khao Yai National Park 1992–2006

		Polyandrous					
	Monoandrous	Serial monogamous	Serial monandrous and EPCs	Serial monandrous and polyandrous	Polyandrous	Polyandrous and EPCs	Serial monoandrous and polyandrous and EPCs
Female	Akira[1] Eclipse[2] Natasha	Rung[3]	Bridget Brit Cassandra	Brenda	Cyrana Daow Hima	Jenna	Andromeda
Total	3	1	3	1	3	1	1

[1] young adult female first seen when still in the natal group; dispersed/disappeared shortly thereafter.
[2] female initially not followed systematically; left after 3 years.
[3] young adult female, matured and subsequently dispersed the year before data collection ceased.

Table 17.3 Mating strategies of wild white-handed gibbon males (Khao Yai National Park, Thailand 1992–2006)

		Polygynous				
	Monogamous	Serial monogamous	Serial monogamous and EPCs	Monogamous and EPCs	Monogamous and EPCs (attempt)	Polygynous
Males	Actionbaby[1]	Chikyu	Bard	Amadeus	David	Christopher[3]
	Chana[2]	Elias	Claude	Efendi		
	Diego	Fearless	Cassius II	Chet[5]		
	Frodo		Marlon			
	Joe					
	Nithat[3]					
	San[4]					
Total	7	3	4	3	1	1

[1] lived successively with two females, but sexual activity was only recorded for one mateship due to irregular observations during previous mateship.

[2] immigrated into the population < 3 years before data collection ceased.

[3] only lived with a female during last 1.5 years of data collection.

[4] delayed dispersal; resident in his natal group.

disappeared shortly after they were first noticed in the population. If I omit individuals from whom I was unlikely to record mating behavior even if it occurred, no mating behavior was recorded for six females and five males. In other words, the majority of adults in the population were sexually active and available for analyses of sexual strategies (68.4%, $n = 19$ females; 79.2%, $n = 24$ males). Two additional unhabituated males were involved in extrapair copulations (EPCs) with a habituated female, but they were not included in analyses of male sexual strategies.

Mating Strategies of Khao Yai Females and Males

Of females seen to copulate ($n = 13$), only three (23.1%) were seen to copulate with a single male, whereas 10 (76.9%) copulated with more than one male, usually two or three males and in one exceptional case (Andromeda) with eight different sexual partners (Table 17.2). Of females seen to copulate with a single sexual partner (i.e., monandrous females) one was a young adult female (Akira) still in her natal group, who dispersed/disappeared soon after her first copulations were noticed (Table 17.2). A second monandrous female (Eclipse) was initially not followed systematically when she lived with two males in a multimale group, and she left after two years. If these two females are set aside, because it is unlikely that their sexual strategies were described comprehensively, it becomes evident that with only one exception adult females at Khao Yai have more than one sexual partner (mean 2.3, SD ± 0.7 partner; excluding Andromeda, who seemed to have had unusually many sexual partners).

Of 10 females sexually active with more than one partner, only one, a young adult female, was observed only in successive partnerships, whereas nine females (90%) were involved in simultaneous mating relationships. Overall, the sexual strategies of Khao Yai females were flexible and diverse (Table 17.2). Of females that were sexually active, five (38.5%) were observed in at least one extrapair copulation, and six (46.2%) maintained simultaneous sexual relationships in multimale groups. Most females engaged in a combination of different sexual relationships during their reproductive careers, i.e., taking part in successive monandrous relationships in combination with extrapair copulations or periods of polyandrous mating in multimale groups or both (Table 17.2). Five of the six females (41.7%) that lived in multimale groups maintained long (>1 year) sexually polyandrous relationships.

Of sexually active males ($n = 19$), seven (36.8%) were monogamous (Table 17.3). However, one of the monogamous males, San, delayed dispersal and was still a resident in his natal group at the end of observations. Another male, Nithat, only lived with a female during the last 1.5 years of data collection. A third male, Chana, immigrated into the population less than three years before data collection ceased. Finally, a fourth monogamous male, Frodo, was known to have lived successively with two females; sexual activity was only recorded during one of these mateships because of irregular observations during his first pairing. After omitting those cases for which documentation of the full array of sexual strategies was unlikely, only 20% of sexually active males ($n = 15$) were monogamous (Table 17.3). Hence, as in females, the majority of adult males of the Khao Yai population engaged in polygamous mating strategies.

Of 12 males with multiple sexual partners, three (25%) were serially monogamous with successive partners. As already seen for females, males' sexual strategies were also variable (Table 17.3). For eight of 12 males (66.6%) their sexual strategy included documented EPCs or once an EPC attempt. Of the males living in multimale groups only one, Diego, was seen to attempt copulating with a neighboring female. Otherwise, all males who achieved extrapair copulations were pair-living at the time. Finally, only one male, Christopher, was seen to be involved in concurrent sexual relationships with two female group members after he had replaced a male and the group's subadult female, Akira, had matured to an adult. Interestingly, only weeks after sexual activity between Christopher and the Akira was noticed, this female disappeared with unknown fate.

For the males living in multimale groups "D" and "J," detailed information on sexual behavior was available for two periods of night-tree-to-night-tree follows (group "D": December 2003–August 2004; group "J": August 2003–December 2004). Copulation success was highly skewed in both groups. In group "D", one male was involved in 88.6% of copulations ($n = 79$) and likewise in group "J" one male achieved the majority of copulations (86.4%; $n = 88$), whereas copulation by the other two males was infrequent (Table 17.3). In both groups, both males had higher copulation rates during the same time periods (Fig. 17.4a,b), except at the end of 2004, when Frodo had a low copulation frequency while Joe copulated frequently (Fig. 17.4b). To attempt to discern which of the males was more likely to have fathered the female's subsequent offspring, I identified the month with the highest conception probability for the two females by back-counting 210 days – the average gestation length in white-handed gibbons – from the infants' births. During the presumed month of the group "D" female's conception, both males copulated with her. The pattern was less clear in group "J": male Frodo was seen to copulate during the month preceding and the month following the most likely period of conception, but during the conception month no copulation was recorded. Given the pattern of copulation around and during females' conception months, both males in multimale groups could have potentially fathered the females' offspring. Hence, a possibility for sperm competition may exist in gibbons. However, before conclusions about sperm competition can be drawn genetic paternity studies must be conducted.

Variable Social Organization and Mating System in Khao Yai Gibbons

The results of my long-term data confirm and extend earlier descriptions of multimale grouping and polyandrous mating at Khao Yai (Reichard 1995b; Sommer and Reichard 2000), and add to a growing body of evidence for a variable social organization and mating system of wild gibbon populations

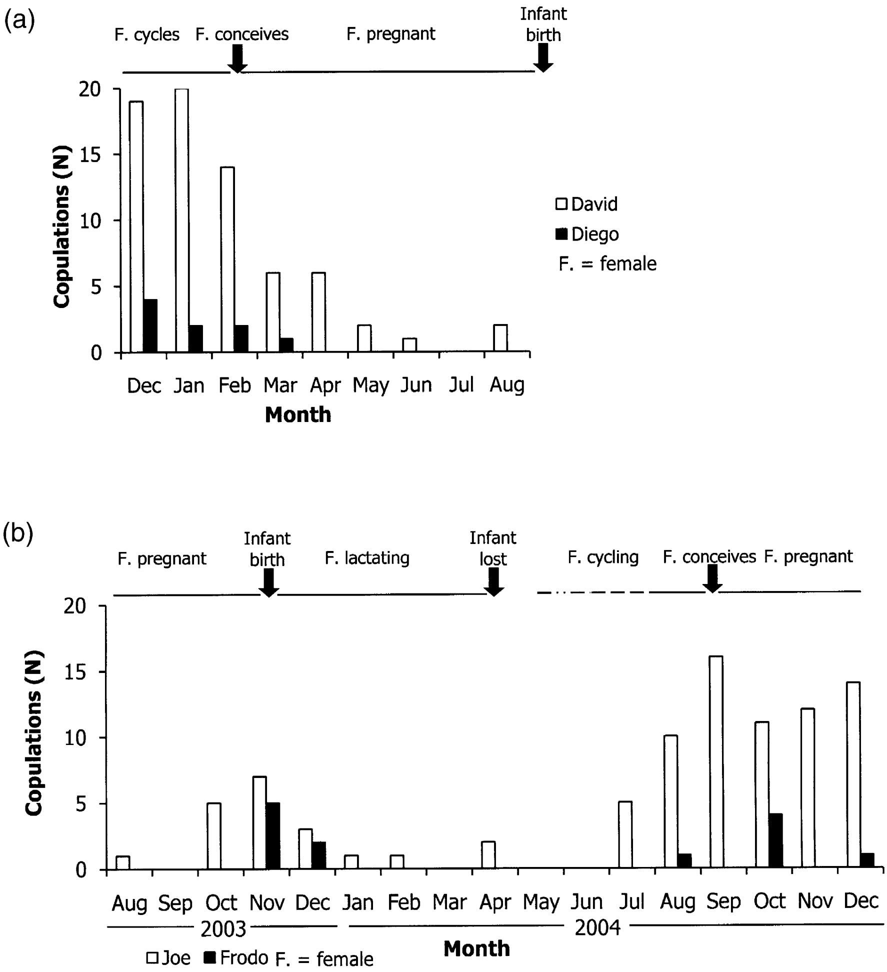


Fig. 17.4 Copulations and reproductive events in multimale groups (**a**) "D" and (**b**) "J", 2003–2004

(Palombit 1992; Fuentes 1999, 2000, 2002; Reichard 2003b; Lappan 2007a,b; Barelli et al. 2008; Malone and White 2008; Reichard and Barelli 2008). This study presents quantitative information on the magnitude of non-monogamous grouping and mating in a hylobatid community, which is important for an understanding of gibbon social dynamics and individual reproductive strategies.

Recognition of a variable social organization has important implications for a comprehensive understanding of gibbon social systems. It is becoming increasingly clearer that gibbon partnerships do not endure for lifetime nor are they terminated primarily by the death of one partner. In my sample, secondary dispersal occurred in males and females, indicating that intrasexual competition for partners and breeding positions does not end with natal dispersal and the formation of a close pair-relationship. Rather, competition continues to be important and permeates individuals' entire reproductive lives.

Four important points emerge from this study. First, the social organization of Khao Yai gibbons extends systematically beyond pair-living. Although pair-living dominated in frequency, and may therefore still be seen as the "modal social structure," a noticeable, stable fraction of about 15% of social groups were multimale, composed of two adult males living and mating for prolonged times with an unrelated adult female. With an adult male group size of two and rarely three, white-handed gibbons at Khao Yai exemplify the smallest possible multimale group structure.

Second, solitary individuals, who have frequently been noticed elsewhere (Mitani 1990a; Cowlishaw 1996), were rare or absent in the Khao Yai population in most census years, as were instances of multifemale grouping. A single, exceptional case of a mixed-species multimale multifemale group was observed. The dominant group types were pair-living and multimale groups. These groups did not reflect individual-specific strategies throughout reproductive careers, but rather flexible responses to changing social dynamics in the population resulting from phenomena such as individuals migrating, dying/disappearing, or aging, which leads individuals to become targets for replacement attempts. Group membership changes repeatedly led to multimale grouping, and many adults experienced periods of pair-living as well as periods of multimale grouping at different times in their reproductive years. These observations corroborate an early, commonly overlooked cautionary note by pioneer Carpenter (1940: 125) who wrote:

> It was found that the family pattern with limited variations characterized gibbon societies. The term 'monogamous mate-ship' might be used [. . .] but this description may be an overgeneralization [. . .]. It has also been shown that there are extra-group individuals which are described as being in a state of transition or as being old isolates.

Carpenter correctly noted that additional adults sometimes reside in gibbon groups and that these individuals were not always of old age. He also clearly and mistakenly thought deviation from the pair-living pattern generally represented a transitional stage. The long-term data from Khao Yai, at least, suggest that multimale units are an alternative grouping strategy to pair-living that potentially persist for periods of a decade or longer.

Third, in contrast to early descriptions of strict monogamy in gibbons (Brockelman and Gittins 1984; Leighton 1987), data on sexual activities of Khao Yai adults who spent sufficiently long periods of their reproductive lives in the population (>3 years) reveal that most adults were polygamous and established serial or simultaneous sexual relationships with more than a single partner (Barelli et al. 2007, 2008; Reichard and Barelli 2008). Additionally, for most sexually monogamous individuals in this study, the full sexual behavior repertoire could probably not be documented due to data limitations. The notion of polygamous sexual strategies in gibbons is consistent with previous records from Khao Yai (Reichard 1995b; Reichard and Sommer 1997; Sommer and Reichard 2000; Reichard 2003b) and recent observations from other gibbon populations (Palombit 1994b, 1996; Lappan 2005, 2007a,b; Malone and White 2008). The observation of an active female role in polyandrous mating behavior is also supported by the recently documented advertisement function of the moderate sexual swelling of white-handed gibbons (Barelli et al. 2007). Like many pair-living birds (Westneat et al. 1990; Griffith et al. 2002) and some mammals (Mason 1966; Hubrecht 1985; Richardson 1987; Sillero-Zubiri et al. 1996; Digby 1999; Fietz et al. 2000; Wolff and Dunlap 2002; Schülke et al. 2004; Morino this volume), Khao Yai gibbons of both sexes strive to maximize reproduction through mating with multiple partners.

Female sexual polyandry is a behavior that gibbons share with other primate females (Hrdy 1986, 2000) and a wide range of other organisms (Keller and Reeve 1995; Zeh and Zeh 1997; Hosken and Stockley 2003; Thom et al. 2004). The relatively high frequency of polyandrous mating in gibbon females is interesting. Since female gibbons cannot be forced to copulate, we must assume that they actively seek additional mating partners. Consequently, advantages that females gain from sexual polyandry should be expected to be substantial (Eberhard 1998) because mating can be costly and, other things being equal, is probably best avoided by females (Daly 1978; Gomendio et al. 1998; Johnstone and Keller 2000; Nunn et al. 2000; Nunn and Altizer 2004).

Fourth, in multimale gibbon groups two adult males are sexually active and copulate with the female. In two groups mating success was highly skewed toward one male, but both males of the group copulated during the same female cycle periods, including around or during the females' fertile phase. However, more data on multimale grouping and especially on female endocrinology and paternity are needed before conclusions can be drawn about the biological and evolutionary importance of female sexual polyandry and multimale grouping in gibbons.

In summary, Khao Yai gibbons were flexible along two axes: (1) social grouping patterns were variable and included pair-living and multimale grouping; and (2) mating relationships were variable with most adults mating polygamously with more than one partner at a time.

The important questions remaining include these: why is such extensive flexibility in grouping and mating observed at Khao Yai, and is the Khao Yai population perhaps exceptional? I believe that the Khao Yai population is not exceptional. What differs is that my data spans a longer period and involves more groups than at other sites. The presence of 14 habituated social groups with mostly adjacent home ranges and their neighbors (Fig. 17.1) allow the investigation of wild gibbon behavior at a community level that is not yet accessible at most other sites (but see Palombit 1992; Lappan 2007a). In gibbons, with their small group size, this type of investigation is a prerequisite to documenting non-pair-living group structures and non-monogamous mating, because otherwise dispersal and migration patterns as well as between-group contacts cannot be studied in detail.

Skeptics may still argue that the situation at Khao Yai is exceptional, because a "crowding effect" resulting from an unusually high population density could perhaps force otherwise pair-living, monogamous individuals to form larger, non-monogamous groups. Such an effect has been suggested for a small African antelope (Arcese et al. 1995) and some co-operatively breeding birds (Stacey and Koenig 1990). Crowding is, however, unlikely to explain the observed behavioral patterns at Khao Yai, because while population density at the site is high, it is within the range of comparable densities reported for other gibbon populations (Leighton 1987; Mitani 1990b; Borries et al. 2002; Yanuar this volume) where flexible grouping and mating has so far not been reported.

Non-monogamous group structures were likewise not attributable to aging of individuals leading to a rare influx of new individuals during periods of "social breakdowns" occurring only after long intervals of stability, as has been previously suggested (Chivers and Raemaekers 1980). Instead, shifts between pair-living monogamy and multimale polyandry occurred repeatedly in both directions during this study; multimale groups sometimes persisted for years, and social change was not primarily caused by deaths or disappearances of aged adults. Instead, immigration of young adult males into established pair-living groups was among the primary causes for the observed social dynamics in the population (Fig. 17.3).

Adaptive explanations for multimale polyandry by females appear straightforward. Generally, females may directly profit from this arrangement through additional food resources or increased paternal investment (Stacey 1982; Dunbar 1995; Põldmaa and Holder 1997; Soltis 1997; Heymann and Soini 1999). They may also profit indirectly through an increasing probability of conception in case of a social mate's temporal or permanent sterility (Gromko et al. 1984), or by producing male offspring with an increased fertilization probability under conditions of sperm competition (Põldmaa and Holder 1997; Yasui 1997; Byers and Waits 2006). Decreased infanticide risk due to paternity confusion (Hrdy 1979; van Schaik and Janson 2000) and doubled infant-protection power from two potential sires are also the potential benefits for females (Borries et al. 1999). Future studies will have to address these possibilities and reveal which positive effects polyandry may have on gibbon females' reproductive success, if any.

In contrast, explaining multimale polyandry from a male perspective appears more difficult because of the general reproductive advantages of polygyny for mammalian males (Williams 1966; Trivers 1972; Parker 1979). Multimale polyandry is rare in mammals and where it exists it often occurs in conjunction with pair-living monogamy. In tamarins for example (Goldizen 1987; Goldizen and Terborgh 1989), multimale polyandry derives from the need for direct paternal investment of more than one male to successfully raise sets of twins or triplets (Goldizen 2003). Such reasoning cannot explain multimale polyandry in white-handed gibbons or other hylobatids. Gibbon females produce a single offspring spaced at long three-year intervals, and direct paternal care in the form of infant carrying is absent in the hylobatid family, with the notable exception of occasional infant carrying by male siamangs (*Symphalangus syndactylus*). But even in siamangs male help may not explain the occurrence of polyandry (Lappan this volume).

Multimale Polyandry, Resource Distribution and Territorial/Female Defense

Multimale polyandry in the absence of direct paternal care may evolve via cooperative territory or female defense, or both. If female reproduction critically depends on the resources of a territory, male territorial behavior (advertisement and defense) may function to attract females and repel competitors (Carranza et al. 1990; Fischer and Fiedler 2001). Under such conditions, a single male may be capable of defending a female, her range, or both as long as female range size is small; when female range size increases, a pair or group of cooperating males may become more successful than a single male (Seddon et al. 2003).

In a recent socioecological study at Khao Yai (Savini et al. accepted), a negative relationship was found between the size and the productivity of gibbon females' home ranges. Across seven groups, larger home ranges were associated with lower productivity than were smaller ranges, and a positive relationship was detected between the time groups spent as polyandrous multimale units and home range size (Savini et al. accepted). On larger, poorer home ranges groups spent more time as multimale polyandrous units than on smaller, richer home ranges.

Perhaps variability in the social organization of Khao Yai gibbons is ultimately linked to the distribution of resources. Data from Khao Yai multimale groups are in agreement with the idea of cooperative male polyandry, because in such groups both males shared sociosexual access to the female. Male participation in social grooming and mating with the female was strongly skewed, allowing identification of a female's primary and secondary male partners (cf. Barelli et al. 2007, 2008). Secondary males were not entirely denied sexual access to the female by the primary males, and one secondary male was seen to copulate with the female during her conception month (Fig. 17.4a). Sexual access by secondary males was probably not a result of a primary male's inability to evict the other male, because replacement following male immigration was common on small home ranges (Fig. 17.3; Savini et al. accepted). Thus, the observations of multimale polyandry are more compatible with mutualism or cooperation, assuming that secondary males have leverage power (Lewis 2002), and that primary males perhaps make reproductive concessions rather than assuming incomplete control (Clutton-Brock 1998). Secondary males may provide a service to primary males such as participation in defending the territory/female against neighboring males, which may ultimately increase a primary male's tenure. Few systematic studies of multimale gibbon groups have yet tested such a hypothesis, but observations from Way Canguk (Lappan 2007a) and Khao Yai multimale groups show that secondary males either alternate or simultaneously engage with primary males in at least some intergroup encounters.

Intergroup encounters in white-handed gibbons are both frequent and potentially harmful (Palombit 1993; Reichard and Sommer 1997). Territorial/female defense may become more costly for a male with higher numbers of neighbors and longer shared borders, both of which may increase as female range size increases. Hence, males living on larger home ranges may experience higher costs for territorial/female defense. In particular, costs of female defense may increase drastically with increasing numbers of male neighbors when females mate polyandrously in the form of EPCs, as observed repeatedly in the Khao Yai population (Reichard 1995b, 2003, this study). Males living on a large home range surrounded by many neighbors may face a tradeoff between an increased need for mate guarding against EPCs and their own motivation to search for additional mating opportunities (Reichard 1995b; Lazaro-Perea 2001). In such a scenario, the benefits to a primary male of having a secondary male to help defend the female against neighboring males' EPC attempts may outweigh the cost of tolerating some copulations of a secondary male. Secondary males would likewise benefit from such arrangement – the low frequency of solitary individuals in this population and their shy behavior suggest that a solitary or "floating" lifestyle is associated with high costs and potentially the lowest reproductive potential. Becoming a secondary male in a polyandrous multimale unit may be a strategy that avoids potentially hazardous transfer, resembling the delayed dispersal of offspring (Brockelman et al. 1998), but with a greater than zero chance of reproduction, at least until a reproductive opening occurs in the neighborhood.

My model for the evolution of grouping and mating flexibility in Khao Yai gibbons is based on a number of assumptions that need to be tested empirically. Most importantly, the contributions of secondary males to intergroup encounters and the influence thereof on a primary male's tenure require critical evaluation. Also a number of basic questions still remain: (1) What are the costs of territory/female defense for gibbon males? (2) What is the relationship between home range size and cost of territory/female defense – does cost increase linearly or exponentially or not at all with moderate increases in range size or number of neighbors? Model calculations have pointed out that a single gibbon male theoretically is capable of defending an area as large as the combined ranges of 5–8 females (van Schaik and Dunbar 1990; Reichard 2003b; but see Bartlett this volume). This suggests that a single male should be capable of defending a territory/female living in a very large range. However, no quantitative study has yet measured actual costs of territorial defense in gibbons. (3) What is the cost of female extrapair copulations to primary males' reproductive success? These and other questions can only be addressed once more multimale gibbon groups are studied.

Sociosexual Flexibility and Advanced Cognitive Abilities

Flexible grouping and mating patterns observed in Khao Yai gibbons and elsewhere (Lappan 2007a; Malone and White 2008) may also be explained as a response to cognitive abilities that were already present in the last common ancestor of gibbons and other apes. In a recent model examining the evolution of great ape cognition, van Schaik et al. (2004) interpreted the flexible social systems and social structures of great apes as part of an evolutionary package associated with the development of a large brain. Van Schaik et al. (2004) argue that great ape sociality is more complex than that of other primates because it shows greater subtlety in dealing with social problems.

As van Schaik et al.'s (2004) model focused specifically on explaining cognitive abilities in great apes, gibbons were not included, perhaps because of the commonly applied simple, static monogamy concept of gibbon social organization that seemed not to fit into a framework of social flexibility and complexity. Gibbon cognition also appears modest at best compared to that of the great apes (Deaner et al. 2006), although interesting similarities in gibbon and great ape cognitive abilities exist (Ujhelyi 2000; Cunningham et al. 2006; Horton and Caldwell 2006). Nevertheless, gibbons and great apes share a recent common ancestry (Hacia 2001), which suggests that it is appropriate to test how gibbons fit into the framework of social commonalities described by van Schaik and colleagues (2004) as distinguishing great apes from other anthropoids. In the following paragraphs, I examine the data presented here in light of van Schaik et al.'s (2004) statements 1–4 highlighting social commonalities in great apes (italicized below).

1. *A tendency toward fission-fusion social organization (or at least toward impermanence of social units), with individuals out of contact with conspecifics for prolonged periods and with foraging females notably solitary*. Gibbons show no tendency toward fission-fusion organization, but neither do gorillas. Gibbons form cohesive groups, although male membership is flexible within limits as groups go through periods of multimale grouping and pair-living. Females clearly forage separately from each other, but they usually remain in the company of a male and flexible choice of association partners seems absent, so far. Thus, gibbon females differ from semisolitary orangutan females. However, the differences between gibbons and great apes may reflect an endpoint of a development along a scale of social flexibility, because not all great apes show a fission–fusion structure nor do females always live solitarily. Variation in female association patterns across chimpanzee populations, for example, is thought to at least partly reflect differences in ecological settings (cf. Boesch and Boesch-Achermann 2000; Wittig and Boesch 2003). The absence of flexible subgrouping in gibbons may be related to selection pressure for small group size and low levels of within-group contest competition rather than a qualitative difference between small and great apes.

2. *Relatively high subordinate leverage*. Observations of intergroup encounters (Reichard and Sommer 1997; Bartlett 2003) and same-sex relationships in

multimale gibbon groups suggest that clearly signaled decided ("formal") dominance relationships are absent in gibbons, despite the potential for clear-cut dominance at least among males in multimale groups. Instead, preliminary data on male–male interactions in multimale groups of Khao Yai gibbons and Way Canguk siamangs (Lappan 2007a) suggest rather cooperative relationships.

3. *Intrasexual bonds among nonrelatives are as common, or more so, than bonds among relatives*. Records of migration patterns in gibbons (Brockelman et al. 1998, this study) suggest that bonding among non-kin occurs in social groups of white-handed gibbons and siamangs (Lappan 2007a) between males but not between females, though again small group size may limit the options of non-kin bonding.

4. *Remarkably extensive intraspecific flexibility in social organization and affiliation*. This study clearly indicates the great potential for flexibility in gibbon social organization with the most prominent forms being pair-living and multimale groupings. Other social compositions were also observed despite their temporal limitations.

Considering the four features of great ape societies listed by van Schaik et al. (2004), gibbons share important social commonalities with other apes. Gibbons also share several other aspects of their biology with great apes (see Fig. 11.2 in van Schaik et al. 2004: 200) such as a slow life history, an arboreal life style, a relatively low vulnerability to predation despite a small body size (Reichard 1998; Uhde and Sommer 2002), a high-quality diet, a tendency toward solitary foraging, and vulnerability to lethal aggression from conspecifics (Palombit 1993; Reichard unpubl. data). The sociosexual flexibility that gibbons at Khao Yai (Sommer and Reichard 2000; Barelli et al. 2007, 2008; Savini et al. 2008) and other sites (Palombit 1994a; Lappan 2007a; Malone and White 2008) share, to some extent with the great apes, may reflect a specific set of cognitive abilities that arose at the time of the last common ancestor between gibbons and great apes, presumably in response to nonsocial selective pressures. That gibbons differ from great apes in specific features is not unexpected and may partly be explained by selective pressures that favored small group size, perhaps as an alternative means of coping with novel social pressures, or may also be interpreted as a reflection of gibbons' more limited cognitive abilities (Deaner et al. 2006). In conclusion, a basic cognitive capacity for solving nonsocial problems with social solutions may have been in place in the last common ancestor of gibbons and great apes, distinguishing them from cercopithecine primates.

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Because group structure variation has not yet been described in gibbons I provide short, descriptive Appendices describing the formation of and social relationships in representative multimale single-female groups (Appendices 1 and 2), a multifemale single-male group (Appendix 3), and the sole multimale multifemale group (Appendix 4). All "father–son" relationships mentioned in Appendices are based on observed *social* parentage of co-residence; genetic relationships were unknown.

Appendix 1: Multimale Single-Female Groups

Multimale groups developed when an adult male immigrated and joined an existing pair ($n = 11$), except once when a multimale unit formed by female-female replacement. In this case, a resident female was replaced by another female; a young adult male group member and his father subsequently both became the female's new partners. Although multimale groups usually formed through male immigration, not all male immigration events resulted in multimale groups because male immigration sometimes led to a rapid male replacement when the former resident male was ousted by the newcomer. Male immigration was competitive and usually accompanied by intense aggression between males, except when a father immigrated into the home range of his son.

With the notable exception of cases where social fathers migrated onto their sons' home ranges, successful immigrants all displaced the resident males from their close relationships with resident females. Male replacement had previously been noticed in this population (Treecuson and Raemaekers 1984; Brockelman et al. 1998), and the Khao Yai long-term monitoring suggests that it amounts to a common cause for group composition changes.

I have observed variable patterns of multimale group formation. Two males in this study, for example, delayed natal dispersal before immigrating into a neighboring group, and an additional observation that closely resembles these cases has been described in detail elsewhere (Brockelman et al. 1998). Another two immigrants were secondary dispersers (one secondary dispersal event occurred after a male was replaced by another immigrant and the other for unknown reasons). An unexpected new pattern observed in this study was males transferring into groups where their sons were the resident males ($n = 2$). In the first case, son Amadeus dispersed from group "A" in 1999 and founded group "T" with the previously solitary female Brenda (Fig. 1). The following year, a new male immigrated into Amadeus' father Fearless' group and replaced Fearless as the female's primary mate (see below). Fearless' group was multimale for about 6 months until Fearless briefly transferred into neighboring group "E" before moving again to join his son Amadeus on home range "T." Before and until shortly after his father's arrival, Amadeus had fiercely resisted immigration attempts by other males, whereas no aggression was observed against his social father. Initially, the female had duetted almost exclusively with Amadeus. Subsequently, however, during a time when Amadeus moved back and forth between his group and neighboring group “SD,” Fearless became the primary duet partner of the female, and remained so even after Amadeus’s permanent return. Social grooming between Fearless and Amadeus had been frequent when they were residents in group “A,” but no grooming was observed between them in group “T,” although both groomed with the female.

In the second case where a social father followed his son, mature son Christopher of group “C” dispersed into group “A” in 2000. About 4 years later, an unknown male immigrated into the group of his father, Cassius II. The immigrant male frequently provoked agonistic interactions with Cassius II. Within a week, Cassius II transferred to group “A” and was accepted by his son Christopher and female Andromeda without hostility. A nearly mature son of Cassius II and brother of Christopher, Chikyū, co-dispersed with Cassius II. Three months later another younger brother, Chuu, likewise transferred into group “A.” The duet pattern in the group remained unchanged after the arrival of the new males, and Christopher is still the regular duet partner of the female at the time of writing. By 2005, Chikyū had reached adulthood, which made the unit the only known multimale gibbon group at Khao Yai with three fully adult (although related) males living with one female. Social relations among the males appear relaxed, and no overt aggression has been noticed, perhaps due to their kinship. Christopher has been seen allogrooming with his younger brothers, who have likewise been groomed by Cassius II, but no allogrooming has been observed between Christopher and Cassius II. All males have been seen allogrooming with female Andromeda.

In multimale group “N” adult males Claude and Nithat were also presumed to be father and son, but unrelated to the immigrant female Hima. After Hima’s arrival in group “N,” she displayed continuous hostility towards resident female Natasha. Hima consistently interfered with Natasha’s foraging, threatened, and chased her. Even though Natasha began lagging behind the group soon after Hima’s appearance, and showed submissive behaviors toward Hima, the young immigrant female continued to dash back and chase Natasha out of fruiting trees. Multiple times Natasha escaped from Hima by descending to the forest floor, which is a very rare behavior in wild gibbons, where she remained cowering while Hima hovered above her. Twice, contact aggression was observed, but more fighting may have occurred, because a few weeks later Natasha disappeared with unknown fate.

Hima began duetting with Nithat, the adult son of the group, when she arrived in the group. During the first days after Hima’s immigration, duets were also still heard from the resident pair Natasha and Claude. However, Hima’s ongoing threats presumably forced Natasha to stop singing shortly thereafter. Hima and Nithat continued to duet, and Claude began to also add replies to Hima’s great calls (for a description of gibbon duet calls see Raemaekers et al. 1984). The males did not overlap with their singing; Nithat would reply first, followed by a less-vigorous response from Claude.

Appendix 2: Multimale Single-Female Group "A"

Male Amadeus of group "T" (described above) tried unsuccessfully to establish polyterritorial polygyny with two females. He was Brenda's pair mate from the summer of 1999. However, in the beginning of 2001, after young female Cyrana immigrated into group "E," joining pileated female Emanuelle and male Bard (see Appendix 3), Amadeus also began traveling with members of group "E." Male Bard was rarely seen with Cyrana and Emanuelle, and Amadeus copulated and sang duets with Cyrana, but also regularly traveled and interacted with Brenda. Repeatedly, Amadeus led Brenda toward the overlapping area between the home ranges of groups "T" and "E." Amadeus appeared to increase group "T's" share of the overlap zone as he foraged ever deeper into group "E's" range. He would then slowly depart from the overlap area and travel even further into group "E's" home range. He emitted contact calls and appeared to wait for Brenda to follow. Brenda rarely crossed deep into "E's" home range and would eventually stay behind when Amadeus proceeded further. Their calling and activity in the overlap area regularly resulted in contact with group "E," and Amadeus was then seen copulating and duetting with Cyrana. Although no quantitative data are available, Amadeus' frequent movement back and forth and simultaneous interactions with the two females gave the impression that he was trying to persuade one of the females to join him and follow onto the other female's home range. He also appeared to try to lead Cyrana toward Brenda and her home range. Cyrana followed him deeper into the group "T" home range than Brenda had followed onto the group "E" home range. However, Cyrana remained cautious and Brenda's constant hostility apparently prevented spatial proximity between the two females and the development of a multifemale group. Brenda frequently threatened Cyrana, and long chases were witnessed during which Brenda pursued Cyrana back onto the "E" home range. Intergroup encounters during this period often exceeded two hours. Eventually, however, Brenda would leave the encounter area and forage away toward the opposite side of her home range. Amadeus often remained, traveled, and spent the night with Cyrana, before he would return to Brenda the following morning or during the day, usually when he heard Brenda singing solo female great calls. One morning, Brenda began calling close to the overlap between her range and that of group "ST." After only a few minutes, a dark male rapidly approached her from the south. The pair copulated and started to duet when suddenly Amadeus brachiated at high speed down the slope and vigorously chased the intruder away. After about two months of changing location and trying to maintain simultaneous socio-sexual relationships with the two spatially separated females, Amadeus ceased traveling with Cyrana and returned to exclusively reside with Brenda. During all this time, Emanuelle had been with Cyrana and Amadeus on most days, but the group's resident male, Bard, was rarely seen with them. There was low-intensity hostility between

Emanuelle and Cyrana and soon after Amadeus ceased traveling with members of group "E," Cyrana emigrated and Bard was seen back with Emanuelle again.

Appendix 3: Multifemale Single-Male Group "J"

Group "J" was identified as multifemale when it was first contacted in November 1998, because two females each carried approximately 2-month-old infants. The group composition remained stable for 26 months until January 2001, when one female and her now-juvenile offspring disappeared with unknown fate. Between November '98 and January '01, the group was contacted on 25 days. Qualitative observations were available for ~25 contact hours despite the females' fear of humans because the adult male of the group, Frodo, was a known, habituated individual born in study group "A" (cf. Brockelman et al. 1998). Frodo dispersed from group "A" in 1990. Between 1991 and 1992 he was encountered a few times with a female of unknown origin (designated as group "K"). During the 1993 census, Frodo was in the company of a new female in the same area as before, but by the end of 1994 both individuals had disappeared. Frodo was rediscovered four years later in group "J."

No hostility was noticed between the females in group "J"; instead, the females were repeatedly observed calmly feeding within 5 m of each other in the same tree crown. The females likewise both tolerated close spatial proximity with each other's infants during feeding and travel as the infants became more independent from their mothers. The females traveled together and in the company of the male on a daily basis and coordinated their movements through contact vocalizations. Their travel pattern resembled those observed in units with other social organizations, e.g., pair-living gibbon groups. Interestingly, both females were heard to sing duets with the male. Neither interfered with the song of the other nor did they sing "in parallel" as typical for maturing daughters with their mothers (cf. Brockelman and Schilling 1984; Raemaekers et al. 1984). Instead, on some days the male first sang a duet with one female and later with the other; on other days, only one of the females duetted with the male during the contact time. Such duet pattern was unique to this group.

Observers did not witness the emigration or death of one of the females and her offspring and the females' social histories were unknown. It is possible that the females were mother and daughter (or sisters) and that Frodo immigrated and displaced the resident male at around the time when the presumably nulliparous daughter reached sexual maturity. Both females may subsequently have copulated and conceived with Frodo and the group remained stable until the onset of a new reproductive cycle when the females' offspring were independent. Female sexual competition is one possible explanation for the disappearance of one of the females. Such a theory of the origin of a multifemale group would parallel the familial polygyny described by Srikosamatara and Brockelman (1987), although in this case the multifemale structure lasted much longer.

Alternatively, two unrelated females may have formed a multifemale group with the male. The presence of two infants, an absence of overt feeding competition, and the females' unusual alternating duet singing with the male, which has never been observed in another gibbon group at Khao Yai or elsewhere, support such interpretation. Delayed female dispersal has in fact been rare in Khao Yai. Still, it remains unclear why one of the females then left after more than a year. Predation or another sudden death appears unlikely, because the female disappeared with her independent juvenile offspring, leaving voluntary emigration the most plausible explanation. Perhaps the benefits of multifemale grouping were outweighed by increasing costs of resource competition and increasing group size, or a better opportunity arose elsewhere?

A pressing question remains: why or how a female could join another female on her territory in the first place? So far, it has forcefully been argued that ecological constraints would not allow gibbons to jump over the poylgyny-threshold and form multifemale groups (Brockelman and Gittins 1984). However, in a recent study Savini et al. (2008) show that female reproduction is less food-limited then previously assumed, which suggests that under the right ecological conditions gibbons may be able to form multifemale groups. More research is needed on other multifemale gibbon groups to illuminate which specific ecological and social conditions allow for the development of socio-sexual multifemale grouping.

Appendix 4: Mixed-Species Multimale Multifemale Group "E"

The mixed-species multimale multifemale group "E" formed after a pair-living female disappeared and the adult male and two immature offspring were first joined by a pileated gibbon female (*H. pileatus*) and then within a few days by a white-handed gibbon female (*H. lar*). Khao Yai National Park marks the eastern distribution border of the subspecies *Hylobates lar entelloides*. The western part of Khao Yai National Park is inhabited by white-handed gibbons, whereas pileated gibbons live in the eastern part. A small hybrid zone exists ~30–40 km east of the Mo Singto – Klong E-Tau research site (Brockelman and Gittins 1984; Suwanvecho 2003). Central Mo Singto has traditionally been believed to be inhabited exclusively by lar gibbons (Brockelman 1975; Raemaekers et al. 1984), but over the years pileated gibbons have occasionally migrated into the Mo Singto – Klong E-Tau area where their species-specific calls are sometimes heard.

The pileated gibbon female was first observed in group "E" in spring 1997 and remains there at the time of writing. Both females of group "E" were adult at the time of their immigration into "E's" home range, but both appeared to be young, presumably nulliparous, judging from their small, nonpendulous nipples. By the end of 1997, the mixed-species trio was joined by a second adult male from the neighborhood, who emigrated after he was replaced by another male. The relationship between the males appeared relaxed and tolerant as no overt aggression – but also no allogrooming – was witnessed between the two. In contrast, relations between the females seemed tense. The pileated gibbon female repeatedly threatened and briefly chased the white-handed gibbon female. The males were not observed to intervene in situations of female hostility, and both females duetted with the males. The white-handed gibbon female emigrated in 1999 and was joined by a recently matured neighboring male. Both animals disappeared from the study site the following year. The pileated female remained with the two white-handed gibbon males until one of them likewise emigrated, changing the structure to pair-living. During the 2005 census, however, the latter pair was again found in the company of a white-handed gibbon female of unknown origin, now as a mixed-species multifemale group.

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