



Social Relationships Among Males In Multimale Siamang Groups

By: Susan Lappan

Abstract

I quantified social and spatial interactions among adults in 4 multimale siamang (*Symphalangus syndactylus*) groups to evaluate the importance of aggression and avoidance in mediating male-male relationships. Actual genetic relationships among adults are unknown, but available mitochondrial data suggest that in 3 of 4 groups, neither male was the offspring or maternal sibling of the female, whereas in the fourth group, a matrilineal relationship between the female and 1 adult male was not excluded. Rates of aggression involving male-male dyads were very low. One male-female dyad maintained closer spatial cohesion than those of other adult dyads in 3 of 4 groups. Nonetheless, all adult males spent substantial percentages of their time ≤ 20 m from other adults in their groups. The percentages of time that male-male dyads spent in social grooming interactions did not differ from those of male-female dyads. In 3 groups, both males copulated with the group female. While previous studies have reported high rates of aggression between adult males and subadult male group members in siamangs, my results suggest that male-male relationships in multimale groups at Way Canguk were relatively harmonious. Acceptance of multimale grouping (and in some cases sexual polyandry) suggests that the benefits outweigh the costs under some circumstances. If there was a genetic relationship between males, then tolerance of delayed dispersal and copulation with the adult female may function as a form of parental investment. Males may also benefit from multimale grouping via enhanced territorial defense or reduced costs of mate defense.

Lappan, S. Social Relationships among Males in Multimale Siamang Groups. *Int J Primatol* 28, 369–387 (2007). <https://doi.org/10.1007/s10764-007-9122-z>. Publisher version of record available at: <https://link.springer.com/article/10.1007%2Fs10764-007-9122-z>

Social Relationships among Males in Multimale Siamang Groups

Susan Lappan

Received: 31 May 2005 / Revised: 4 October 2005 / Accepted: 27 February 2006 /

Published online: 18 May 2007

© Springer Science + Business Media, LLC 2007

Abstract I quantified social and spatial interactions among adults in 4 multimale siamang (*Symphalangus syndactylus*) groups to evaluate the importance of aggression and avoidance in mediating male-male relationships. Actual genetic relationships among adults are unknown, but available mitochondrial data suggest that in 3 of 4 groups, neither male was the offspring or maternal sibling of the female, whereas in the fourth group, a matrilineal relationship between the female and 1 adult male was not excluded. Rates of aggression involving male-male dyads were very low. One male-female dyad maintained closer spatial cohesion than those of other adult dyads in 3 of 4 groups. Nonetheless, all adult males spent substantial percentages of their time ≤ 20 m from other adults in their groups. The percentages of time that male-male dyads spent in social grooming interactions did not differ from those of male-female dyads. In 3 groups, both males copulated with the group female. While previous studies have reported high rates of aggression between adult males and subadult male group members in siamangs, my results suggest that male-male relationships in multimale groups at Way Canguk were relatively harmonious. Acceptance of multimale grouping (and in some cases sexual polyandry) suggests that the benefits outweigh the costs under some circumstances. If there was a genetic relationship between males, then tolerance of delayed dispersal and copulation with the adult female may function as a form of parental investment. Males may also benefit from multimale grouping via enhanced territorial defense or reduced costs of mate defense.

Keywords aggression · flexible grouping and mating · gibbon · polyandry

Introduction

Until recently, researchers considered gibbon social organization, described as social monogamy with territoriality (Leighton 1987), to be relatively invariant. However, a growing body of evidence suggests that forms of gibbon social organization other

S. Lappan (✉)

Department of Anthropology, San Diego State University,
3032 Macaulay St., San Diego, CA 92106, USA
e-mail: lappan@nyu.edu

than social monogamy can occur. A recent review noted numerous reports of gibbon groups containing >2 adults (Fuentes 2000), and in 3 groups of white-handed gibbons (*Hylobates lar*) at Khao Yai, 2 adult male group members copulated with the group female (Brockelman *et al.* 1998; Sommer and Reichard 2000), illustrating that gibbon social and mating patterns display considerable flexibility. However, researchers have not yet examined patterns of social interaction among adults in gibbon groups containing >2 adults in detail. I collected behavioral data from adults in multimale siamang groups at the Way Cangkuk Research Station in southern Sumatra to explore the roles of aggression, avoidance, and affiliation in mediating social relationships among males.

Researchers have described intrasexual aggression as playing a role in maintaining socially monogamous grouping in several primate taxa (*Callicebus moloch*: Fernandez-Duque *et al.* 1997; *Hylobates agilis*: Gittins 1979, 1980; Mitani 1987; *H. klossii*: Tenaza 1975; Tilson 1981; *H. lar*: Carpenter 1940; Palombit 1993; Raemaekers and Raemaekers 1985; Reichard and Sommer 1997; *H. muelleri*: Mitani 1984), including siamangs (Chivers 1974; Chivers and Raemaekers 1980). The observation of multimale grouping therefore raises questions about how relationships between male group-members are managed, and about the costs and benefits of multimale grouping for gibbon males. If the costs of multimale grouping exceed the benefits for 1 or both males, then they should either emigrate or seek to restore unimale grouping by evicting the second males. High rates of aggression involving male-male dyads in multimale groups may therefore reflect a conflict of interest between males regarding the maintenance of multimale grouping. Aggression between males reduces the copulation rate of subordinate male African wild dogs in cooperatively polyandrous societies (Creel and Creel 2002), suggesting that aggression may also be important in mediating mating competition between males in polyandrous mammalian groups, even when both males benefit from multimale grouping. Therefore, frequent aggression in a sexual context, coupled with a clear male dominance hierarchy, suggests that aggression is functionally important in mediating male-male mating competition. If ≥ 1 male in a multimale group benefits from multimale grouping, then they may seek to avoid aggression by avoiding close proximity with the second male, while nonetheless maintaining cohesion with the social group. Accordingly, Schaffner and French (2004) report a pattern of avoidance between males in polyandrously mating marmosets, coupled with low rates of aggression. If both males benefit from multimale grouping, then males may cooperate to promote shared interests. If neither high rates of aggression nor avoidance among males occurs, then it is reasonable to conclude that the benefits of multimale grouping may be equal to or greater than the costs for each male given their ecological and social circumstances.

Methods

Study Area

The Way Cangkuk Research Station is located in the Bukit Barisan Selatan National Park on Sumatra, Indonesia, at 50 m above sea level. The research area, which is run collaboratively by the Wildlife Conservation Society-Indonesia Program (WCS-IP)

and the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA), encompasses 900 ha of forest. A 165-ha area in the southeast portion of the study area was damaged by fire associated with the El Niño–Southern Oscillation (ENSO) event of 1997. The home ranges of 36 groups of siamangs are wholly or partially within the research area.

My study involved 3 multimale siamang groups (A, B, and F) with home ranges consisting entirely of primary forest, and a fourth multimale group (C) with a home range including both primary and fire-damaged forest. O'Brien *et al.* (2003) found significantly higher frequencies of reproductive-sized strangling figs in siamang home ranges consisting entirely of primary forest than in home ranges containing fire-damaged areas, which suggests that fire-damaged areas are poorer quality habitat for siamangs. Mean home range size in undamaged areas was also larger than in burned areas, but not significantly so (O'Brien *et al.* 2003). However, C was an outlier, having the second-largest home range recorded, and retaining a high density and frequency of figs and other important food species (O'Brien *et al.* 2003), suggesting that the quality of habitat in C's home range remains high.

Way Cangkuk siamangs have been the subjects of demographic and behavioral studies since 1998 (O'Brien *et al.* 2003). Siamang group density in the unburned portion of the study area is high, at *ca.* 4.11 groups/km² (O'Brien *et al.* 2003), relative to the mean density of $2.6 \pm .73$ groups/km² in the National Park (O'Brien *et al.* 2004) and to densities reported from other siamang study sites (Chivers 1974; Gittins and Raemaekers 1980; West 1981). No siamang group at Way Cangkuk had a home range consisting entirely of fire-damaged habitat.

Rainfall in the study area is weakly seasonal, but there is no significant relationship between rainfall and fruit crop in the study area (Kinnaird and O'Brien 2005). Though fig and nonfig fruit availability varied between months, fig and nonfig fruit crops at Way Cangkuk displayed no pronounced seasonal variation from 2000 to 2002 (Kinnaird and O'Brien, *unpubl. data*).

Study Groups

I collected data from 4 habituated siamang groups that are known to have been multimale since 1998 (M. Prasetyaningrum, *pers. comm.*). Group compositions in March 2001 are in Table I. All individuals were recognizable based on facial and body features.

Table I Composition of groups A, B, C, and F in March 2001

Group	Adult		Subadult Female	Juvenile		Infant	Total
	Female	Male		Large	Small		
A	AMA	AMI, AMU				ARJ(m)	4
B	BAM	BMO, BAR		BRA(m)	BIM(m)	BMG(m)	6
C	CON	CGO, CKR		CBR(m)		CHE(f)	5
F	FRI	FRE, FRA	FUL ^a	FIF(f)		FRN(f)	6

^a Subadult female FUL emigrated in May 2002.

I classified individuals as infants, juveniles, subadults, or adults based on several features. Infants are very small individuals that were at least partially dependent on adults for transportation. Juveniles had a smaller body length than adults, and were noticeably immature in their facial features, but were independent of adults for transportation. I subdivided the juvenile class into large juveniles and small juveniles based on body size. The large juvenile at Way Canguk is equivalent to Palombit's (1992) adolescent.

I distinguished adult and subadult females based on evidence of parity, including elongated nipples and the presence of a clinging infant. In groups containing more than one adult-sized female, I described females without infants or elongated nipples as subadult.

Palombit (1992) described subadult male siamangs as appearing "less robust in the upper torso than adult males, although they are of similar overall body length." However, in the study groups, no male fit this description. All adult-sized males displayed canines of similar size and had mature-looking faces, suggesting that they were older than subadult male siamangs described from other sites. Adulthood in gibbons is often described as a social, rather than a physical condition, with an adult male being "paired to a [female] with whom it defends a territory, duets, coordinates activity, and reproduces" (Palombit 1992). However, at Way Canguk, all large males participated in territorial defense, including duetting and counter-calling activities and aggression during intergroup encounters. All males also coordinated activity with females, though to varying degrees. In A, B, and C, 2 males also copulated with the female. Therefore, there was no obvious physical or social cue by which I could distinguish males in multimale groups, and I tentatively designated all physically adult-appearing males in A, B, C, and F as adult. However, given the absence of information about group compositions before 1998, my use of the term adult does not reflect an assumption that the individual has dispersed from the natal group. I employ the term subadult male only when discussing males classified as such by researchers at other sites.

Actual geneological relationships among adult group members are not known, and genetic data from nuclear loci are not currently available. However, a 350 base-pair sequence of the Hypervariable 1 (HV1) region of mitochondrial DNA from each adult in the study group is available from a concurrent study of dispersal patterns in siamangs (Lappan 2007). I describe DNA collection and sequencing methods in detail in Lappan (2007). As mitochondrial data are maternally inherited, close matrilineal relatives, e.g., mother and offspring, maternal siblings, should have identical sequences unless there has been a spontaneous mutation. In A, B, and C, the haplotype of each adult differed from that of each other adult group member by ≥ 2 base pairs (Table II). However, in F, 1 male (FRA) had a haplotype identical to that of the adult female FRI (Table II). If the mutation rate of siamang DNA in this region is similar to those of other hominoids, then the probability of a sequence difference of ≥ 2 base pairs between mother and offspring in a region of this size is *ca.* $4.9 \cdot 10^{-5}$ (Howell *et al.* 2003). Accordingly, I conclude that neither adult male in A, B, or C could have been the offspring of the adult female, and that none of the adults in these groups were maternal siblings, whereas adult male FRA could have been the offspring of FRI or her maternal sibling.

Behavioral Observations

Three field assistants and I collected behavioral data during sleeping-tree-to-sleeping tree follows. I collected data from group A from March 2001 to December 2001, from group B from March 2001 to August 2002, from group C from June 2001 to February 2002, and from group F from February 2002 to August 2002. I included data collected by field assistants only after ≥ 3 mo of training and repeated verification of interobserver reliability in side-by-side data collection. Observers collected data in pairs. On each day, we selected an adult individual as the focal individual on a rotating basis. We followed each group until each adult had served as the focal individual for 2 d when possible, and we followed groups on a rotating basis. We recorded instantaneous samples of focal individual activity, nearest neighbor distance and identity (excluding infants), and interindividual distance with each other adult group member at 5-min intervals. We recorded all copulations, attempted copulations, and incidents of aggression. We calculated daily path lengths by pacing below the focal individual.

Adult male AMU emigrated from A in December 2001, and was subsequently contacted as the lone male in a neighboring group. Adult male CKR disappeared from C in February 2002, and was not relocated. I included only data collected while the groups were still multimale. B and F remained multimale through July 2005. Observational data available for each group and focal individual are in Table II.

I examined the importance of avoidance among males by comparing spatial relationships among male-male dyads with those of other adult dyads in the same

Table II Summary of behavioral data available for each focal adult, with HV1 haplotypes

Group	Individual	Sex	HV1 haplotype	Days ^{a,c}	Mean hours/day ^{b,c}
A	AMI	Male	10	13	9.2
	AMU	Male	2	9	9.4
	AMA	Female	11	12	9.3
B	BMO	Male	2	24	9.8
	BAR	Male	4	18	9.8
	BAM	Female	3	22	10.6
C	CGO	Male	5	13	9.0
	CKR	Male	7	10	10.3
	CON	Female	6	12	10.6
F	FRE	Male	2	10	9.7
	FRA	Male	1	8	9.9
	FRI	Female	1	10	10.5

^a Days in which ≥ 5 h of general activity data are available for the focal individual.

^b Hours in which $\geq 25\%$ of instantaneous general activity data are available for the focal individual.

^c As each analysis excluded hours and days on the basis of availability of data involving the variable of interest, instead of the availability of general activity data, analyses of some behavioral variables may include fewer days. For some variables, e.g., interindividual distance, dyadic grooming interactions, I grouped equivalent data from different focal individuals, e.g., focal AMI grooms AMA is equivalent to focal AMA is groomed by AMI.

groups. If males in multimale groups employed avoidance to avert aggression, then other adult dyads should display closer spatial cohesion than male-male dyads.

I evaluated spatial relationships among adults using the variable mean percentage of time during which each group member (excluding the infant) was the focal adult's nearest neighbor, and 2 independent measures of interindividual distance.

In some instantaneous samples, the observers could not determine interindividual distances because 1 individual was not visible. The distance at which an individual is visible varies depending on forest structure, the phenological state of the intervening plants, and the individual's activity. In the vast majority of cases in which observers following a focal individual could not locate another individual for instantaneous sampling, they ultimately discovered the missing individual >20 m from the focal individual. Thus 20 m may represent a physical limit past which observers could not reliably determine interindividual distances. To avoid bias, I employed the variable mean percentage of time spent ≤ 20 m from another individual to estimate the tendency of pairs of individuals to range together and excluded data when observers recorded interindividual distances of >20 m from analyses of interindividual distance. The modified measure of mean interindividual distance does not reflect overall patterns of space use, but instead is sensitive only to differences generated by the tendency of individuals that are ranging ≤ 20 m from each other to approach or to avoid one another.

Because intragroup feeding competition can affect patterns of interindividual spacing, I also repeated analyses of time spent ≤ 20 m from other adults and mean interindividual distance excluding data collected during feeding bouts.

I employed the variable mean percentage of time spent in social grooming interactions to estimate the importance of affiliative interaction for each adult dyad. It was not possible to collect data on the direction of approaches or initiation of interaction between individuals (Hinde 1983). Therefore, I used the direction of grooming interactions to examine the issue of reciprocity between members of male-male dyads.

I conducted analyses using the daily means of hourly proportions of time (or hourly means, for interindividual distance) as units of analysis. I included hours if $\geq 25\%$ of relevant data were available, and days were included if ≥ 5 h of data were available. As the data missing in instantaneous samples differed between variables, sample sizes differed among analyses. All group members almost invariably slept in the same or adjacent sleeping trees, and estimated day lengths typically differed by <15 min. Therefore, where data collected from different focal adults were equivalent, e.g., interindividual distance between focal BAR and BMO and interindividual distance between focal BMO and BAR, I grouped all available data for analyses. Analyses of nearest neighbor relationships in F were complicated by the emigration of subadult female FUL in May 2002, which reduced the number of potential nearest neighbors. To address the problem, I included only data collected after the emigration of female FUL in the analyses.

Using daily means as units of analysis requires the assumption that daily means represent independent samples of the behavior of an individual or dyad. To evaluate this assumption, I conducted runs testing on the differences between each daily mean in the series and the median for each variable. No significant temporal clustering of mean daily values occurred for any variable (percentage of time as nearest neighbor: AMI-AMA: $Z=1.312$, $N=11$, $p=.189$; AMU-AMA: $Z=.040$, $N=9$, $p=.968$; AMI-

AMU: $Z=1.312$, $N=11$, $p=.189$; AMU-AMI: $Z=.040$, $N=9$, $p=.968$; BMO-BAM: $Z=-1.529$, $N=22$, $p=.126$; BMO-BAR: $Z=-.218$, $N=22$, $p=.827$; BAR-BMO: $Z=1.020$, $N=17$, $p=.308$; BAR-BAM: $Z=-1.494$, $N=17$, $p=.135$; CGO-CON: $Z=.029$, $N=11$, $p=.977$; CGO-CKR: $Z=.029$, $N=11$, $p=.977$; CKR-CGO: $Z=1.006$, $N=10$, $p=.314$; CKR-CON: $Z=-.335$, $N=10$, $p=.737$; FRE-FRI: $Z=.000$, $N=8$, $p=1.000$; FRE-FRA: $Z=-1.146$, $N=8$, $p=.252$; FRA-FRE: $Z=.382$, $N=6$, $p=.703$; FRA-FRI: $Z=1.146$, $N=8$, $p=.252$; percentage of time <20 m apart: AMI-AMA: $Z=.012$, $N=19$, $p=.809$; AMU-AMA: $Z=.015$, $N=17$, $p=.819$; AMI-AMU: $Z=-.689$, $N=20$, $p=.484$; BMO-BAM: $Z=-.469$, $N=42$, $p=.643$; BAR-BAM: $Z=-1.480$, $N=38$, $p=.137$; BMO-BAR: $Z=-.160$, $N=40$, $p=.876$; CGO-CON: $Z=-.887$, $N=21$, $p=.370$; CKR-CON: $Z=-.689$, $N=20$, $p=.484$; CGO-CKR: $Z=-.887$, $N=21$, $p=.370$; FRE-FRI: $Z=.259$, $N=16$, $p=.810$; FRA-FRI: $Z=.259$, $N=16$, $p=.810$; FRE-FRA: $Z=1.294$, $N=16$, $p=.200$; mean interindividual distance: AMI-AMA: $Z=.960$, $N=19$, $p=.243$; AMI-AMU: $Z=-.488$, $N=17$, $p=.617$; AMA-AMU: $Z=.776$, $N=16$, $p=.429$; BMO-BAM: $Z=.469$, $N=42$, $p=.643$; BMO-BAR: $Z=-.193$, $N=28$, $p=.853$; BAM-BAR: $Z=-.193$, $N=28$, $p=.853$; CGO-CON: $Z=-.887$, $N=21$, $p=.370$; CGO-CKR: $Z=-1.909$, $N=8$, $p=.057$; CON-CKR: $Z=-.991$, $N=17$, $p=.315$; FRE-FRI: $Z=.259$, $N=16$, $p=.810$; FRE-FRA: $Z=.000$, $N=13$, $p=1.000$; FRI-FRA: $Z=-.835$, $N=14$, $p=.417$). Therefore, I assumed the daily means to be independent. I arcsine transformed all proportional data before conducting parametric statistical tests. All tests were 2-tailed.

Results

Duetting

Researchers have described the production of siamang vocal duets as a pair-bonding behavior (Geissmann 1999; Geissmann and Orgeldinger 2000). However, most studies of vocal behavior have involved captive siamangs living in pairs with immature offspring. Geissmann (1999) reported incorporation of a third adult performer into the duets of adult pairs of captive siamangs. Therefore, it is unclear what patterns of vocal behavior should be expected in wild siamang groups with retained adult offspring or additional adult immigrants. In my study, all adult-sized individuals—including the subadult female—participated in all group duets, with same-sex adults performing the sex-specific portions of the duet simultaneously.

Aggression

Overall rates of aggression in the study groups were low ($.27 \pm .08$ aggressive interactions/group per day) compared with the rate of 1.5 aggressive interactions/group per day reported from Kuala Lompat (Chivers 1974), the only siamang study site from which comparative data are available. At Way Canguk, male-male dyads did not display particularly high rates of aggressive interaction relative to those displayed by other adult dyads (Table III), and rates of aggression between adult males were dramatically lower than the .73 aggressive interactions/day in an adult male-subadult male dyad at Kuala Lompat. Rates of aggression were too low to permit analysis of dominance relationships among males.

Table III Incidents of aggression involving adults in groups A, B, C, and F

Group (days ^a)	Dyad	N (events/day)	Context		Aggressor (N) (where clear)	Winner ^c (N) (where clear)
			Feeding	Nonfeeding ^b		
A (42)	Female AMA and male AMI	2(.05)	2	0	AMA (1) AMI (1)	AMA (1) AMI (1)
	Female AMA and male AMU	2(.05)	2	0	AMA (2)	AMA (2)
	Male AMU and male AMI	5(.12)	3	2	AMI (2) AMU (1)	AMI (2)
B (79)	Male BMO and female BAM	5(.06)	3	2	BAM (3)	BAM (3)
	Male BAR and female BAM	1(.01)	1	0	-	BAM (1)
	Male BMO and male BAR	3(.04)	1	2	BMO (2)	BMO (1) BAR (1)
C (59)	Female CON and male CGO	3(.05)	2	1	CON (2)	CGO (1) CON (1)
	Female CON and male CKR	1(.02)	1	0	-	CON (1)
	Male CGO and male CKR	2(.03)	1	1	CGO (1)	CGO (1)
F (54)	Female FRI and male FRE	2(.04)	1	1	-	FRI (1)
	Female FRI and male FRA	0(.00)	0	0	-	-
	Male FRE and male FRA	1(.02)	1	0	-	FRE (1)

^a Aggression data are available from A from January 2000 to December 2000, from B from November 2000 to August 2002, from C from October 2000 to February 2002, and from F from March 2001 to August 2002. All available data are included in analyses of aggression. Days = the number of days of observational data for aggression available for each dyad. The figures differ from the numbers of observational data available for other analyses in the study.

^b Nonfeeding contexts include grooming, travel and rest. Aggression was never observed in the context of sexual activity.

^c Victory is retention of the contested resource or failure to move ≥ 2 m from the location of the aggressive interaction.

In Palombit's (1992, 1994a) study of siamangs in northern Sumatra, 2 of 5 extrapair copulations between adult females and male members of neighboring groups were terminated by aggression from the female's pair-mate. All extra-pair copulations not resulting in aggression occurred at a distance of >20 m from the female's pair-mate (Palombit 1992), which suggests that the copulations may have escaped the attention of the cuckolded male. However, I never observed aggression toward a mating pair, though several copulations occurred ≤ 20 m from the uninvolved male, a distance at which observation by the other male was generally possible. On most occasions, the uninvolved male oriented to the copulating pair, but displayed no other visible reaction.

Spatial Relationships Among Males

Nearest Neighbor Relationships

In A, the mean percentage of time that each male spent as the other's nearest neighbor did not differ from that expected (Table IV).

In B, the mean percentage of time that male BMO spent with adult male BAR as his nearest neighbor is significantly lower than expected based on the number of individuals in the group (Table IV). However, the mean percentage of time that BAR spent with BMO as his nearest neighbor was actually higher than expected (Table IV).

In C, the percentage of time that male CGO had male CKR as his nearest neighbor was significantly lower than expected, whereas the percentage of time that CKR had CGO as his nearest neighbor does not differ significantly from that expected (Table IV).

Similarly, in F, male FRA was male FRE's nearest neighbor for a significantly lower mean percentage of time than expected, whereas the percentage of time that FRE was FRA's nearest neighbor does not differ significantly from that expected (Table IV). Because the data set is very small for F, sampling of this variable may not have been adequate to detect real differences.

Percentage of Time ≤ 20 m from Other Group Members

There was ≥ 1 other group member ≤ 20 m from each adult male $\geq 61\%$ of the time, and in A and B the mean percentage of time that each male was ≤ 20 m from another group member was $>75\%$ (Fig. 1). However, CKR and FRA spent substantially lower percentages of time ≤ 20 m from their nearest neighbors than did other males in this study.

In A, there is no significant difference among adult dyads in mean percentages of time spent <20 m apart (ANOVA: $F_{2,51}=.265$, $p=.768$; Fig. 2). However, if feeding

Table IV Actual and expected mean percentage of each adult male's time during which the other adult male in his group was his nearest neighbor

Group	Male	Mean percentage of time	Expected percentage of time ^a	<i>N</i>	<i>t</i>	Significance
A	AMI	47.0	50.0	10	0.349	$p=0.734$
	AMU	43.5	50.0	9	-0.156	$p=0.880$
B	BMO	13.5	25.0	22	-3.278	$p=0.004^*$
	BAR	34.2	25.0	17	5.843	$p<0.001^*$
C	CGO	10.4	33.3	11	-6.165	$p<0.001^*$
	CKR	25.7	33.3	8	-0.303	$p=0.769$
F	FRE	10.4 ^b	33.3 ^b	6	-6.253	$p=0.002^*$
	FRA	21.2 ^b	33.3 ^b	4	-2.490	$p=0.088$

Analysis was via 1-sample *t*-test.

^aI calculated the expected percentage as 100% divided by the number of other group members (excluding infants).

^bAnalyses for group F include only samples collected after the emigration of subadult female FUL.

* $p<0.05$ level

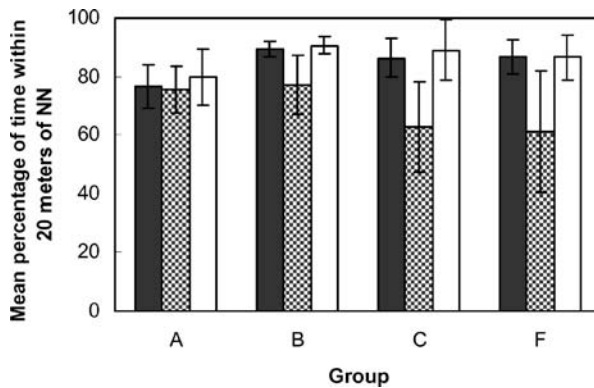


Fig. 1 Mean percentage of time that each adult was ≤ 20 m from its nearest neighbor (mean \pm 95% confidence intervals). Black bars represent males AMI, BMO, CGO, and FRE; stippled bars represent males AMU, BAR, CKR, and FRA; and white bars represent females AMA, BAM, CON, and FRI.

data are excluded, then the dyad consisting of 2 males spent significantly less time < 20 m apart than did other adult dyads (ANOVA with Bonferroni-corrected multiple comparisons: $F_{2,51} = 4.606$, $p = .015$; AMI-AMA and AMI-AMU: $p = .033$, AMI-AMA and AMU-AMA: $p = 1.000$, AMI-AMU and AMU-AMA: $p = .042$).

However, in B, C, and F, there are significant differences among adult dyads in mean percentages of time spent < 20 m apart (ANOVA: B: $F_{2,119} = 21.377$, $p < .001$; C: $F_{2,61} = 29.398$, $p < .001$; F: $F_{2,47} = 17.980$, $p < .001$). Bonferroni-corrected multiple comparisons suggest that in each group, a single male-female dyad spent significantly more time < 20 m apart than all other adult dyads did (Table V; Fig. 2). In each of these groups, excluding feeding data does not change the significance or direction of differences among adult dyads (ANOVA with Bonferroni-corrected multiple comparisons: B: $F_{2,119} = 16.888$, $p < .001$; BMO-BAM and BMO-BAR: $p < .001$, BMO-BAM and BAR-BAM: $p < .001$, BMO-BAR and BAR-BAM: $p = 1.000$; C: $F_{2,61} = 22.751$, $p < .001$, CGO-CON and CGO-CKR:

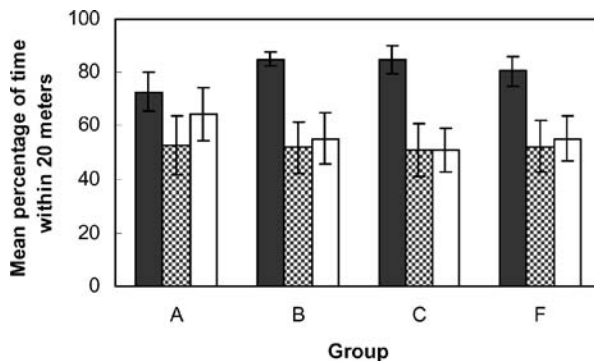


Fig. 2 Mean percentage of time that adults spent ≤ 20 m from each other (mean \pm 95% confidence intervals). Black bars represent the following dyads: male AMI and female AMA, male BMO and female BAM, male CGO and female CON, and male FRE and female FRI. Stippled bars represent dyads consisting of 2 adult males. White bars represent the following dyads: male AMU and female AMA, male BAR and female BAM, male CKR and female CON, and male FRA and female FRI.

$p < .001$, CGO-CON and CKR-CON: $p < .001$, CGO-CKR and CKR-CON: $p = 1.000$; F: $F_{47} = 12.442$, $p < .001$, FRE-FRI and FRE-FRA: $p < .001$, FRE-FRI and FRA-FRI: $p < .001$, FRE-FRA and FRA-FRI: $p = 1.000$).

Mean Interindividual Distance

In A, there is no significant difference among the mean interindividual distances of adult dyads (ANOVA: $F_{2,51} = .265$, $p = .768$; Fig. 3). If time spent feeding is excluded, the differences remained insignificant (ANOVA: $F_{2,51} = .191$, $p = .827$).

However, in B, C, and F, mean interindividual distances differed significantly among adult dyads (ANOVA: group B: $F_{2,97} = 8.198$, $p = .001$; group C: $F_{2,45} = 11.204$, $p < .001$; group F: $F_{2,42} = 9.611$, $p < .001$). Bonferroni-corrected multiple comparisons suggest that in each group, 1 male-female dyad maintained significantly shorter mean interindividual distances than all other adult dyads did (Table V; Fig. 3). If time spent feeding is excluded, mean interindividual distances of adult dyads in all 3 groups still differ significantly (ANOVA with Bonferroni-corrected multiple comparisons: B: $F_{2,97} = 7.341$, $p < .001$; BMO-BAM and BMO-BAR: $p = .002$, BMO-BAM and BMO-BAR: $p = .025$, BAR-BMO and BAR-BAM: $p = 1.000$; C: $F_{2,41} = 5.257$, $p = .010$; CGO-CON and CGO-CKR, $p = .015$, CGO-CON and CKR-CON: $p = .087$, CGO-CKR and CKR-CON: $p = .860$; F: ANOVA: $F_{2,42} = 8.448$, $p = .001$; FRE-FRI and FRE-FRA, $p = .015$, FRE-FRI and FRA-FRI, $p = .001$, FRE-FRA and FRA-FRI $p = 1.000$). The direction of differences is identical to those in analyses including time spent feeding for B and F. However, in C, there are significant differences only between the dyads CGO-CON and CGO-CKR.

Grooming Relationships Among Adults

In A, there were significant differences among adult dyads in mean percentages of time spent grooming (ANOVA: $F_{2,55} = 5.253$, $p = .008$). Bonferroni-corrected

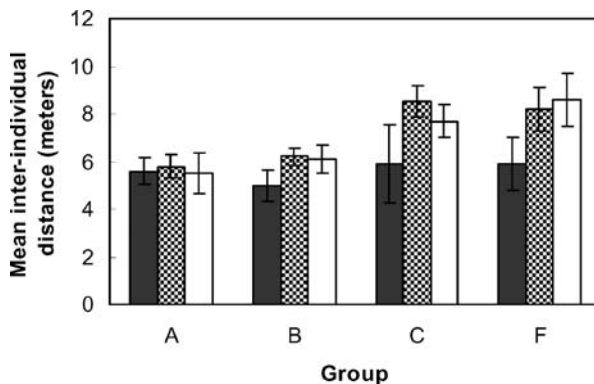


Fig. 3 Mean interindividual distance (m) when the individuals involved were ≤ 20 m from each other (mean \pm 95% confidence intervals). Black bars represent the following dyads: male AMI and female AMA, male BMO and female BAM, male CGO and female CON, and male FRE and female FRI. Stippled bars represent dyads consisting of two adult males. White bars represent the following dyads: male AMU and female AMA, male BAR and female BAM, male CKR and female CON, and male FRA and female FRI.

multiple comparisons suggest that the dyad consisting of male AMI and female AMA spent a significantly higher mean percentage of time grooming than the dyad of male AMU and female AMA did (Table V; Fig. 4). However, the dyad of the 2 adult males did not spend a significantly different proportion of time grooming than either male-female dyad did (Table V). In B, C, and F there is no significant difference among adult dyads in the percentage of time spent grooming (ANOVA: B: $F_{2,121}=2.144$, $p=.122$, C: $F_{2,61}=.815$, $p=.448$, F: $F_{2,47}=.603$, $p=.552$; Fig. 4).

In all 4 groups, the percentage of time that the first male spent grooming the second does not differ significantly from the percentage of time that the second male spent grooming the first (ANOVA: A: $F_{1,39}=.083$, $p=.774$; B: $F_{1,79}=.181$, $p=.672$; C: $F_{1,41}=.087$, $p=.769$; F: $F_{1,31}=.1101$, $p=.753$), which suggests that social grooming effort among males was generally reciprocated.

Mean Daily Path Length

If some males traveled further in search of food or spent more time patrolling the boundaries of their territories than other adults did, then they should have longer mean daily path lengths. However, there is no significant difference among adult mean daily path lengths in any group (ANOVA: A: $F_{2,23}=3.208$, $p=.061$, B: $F_{2,50}=.022$, $p=.979$, C: $F_{2,29}=.401$, $p=.674$, F: $F_{2,22}=.380$, $p=.688$).

Copulations

We observed a total of 38 copulations, of which 36 involved adult females, and 2 involved a subadult female. In A, B, and C, both males copulated with the adult female, whereas in F, only 1 male copulated (Table VI). The numbers of copulations in A and F are too low to permit statistical comparisons between male copulation frequencies. However, in B, male BMO, though unable to monopolize copulations, participated in a significantly higher proportion of copulations than predicted by chance (χ^2 test: $\chi^2_1 = 4.765$, $p<.05$). Conversely, in C, the distribution of copulations across males does not differ from that predicted (χ^2 test: $\chi^2_1 = .77$, $p=.782$).

Discussion

Flexible Grouping in Hylobatids

Though hylobatids are generally socially monogamous, there are numerous reports of gibbon groups containing ≥ 3 adults (*Hoolock hoolock*: Ahsan 1995, 2000; Siddiqi 1986; *Hylobates lar*: Brockelman *et al.* 1998; Carpenter 1940; Sommer and Reichard 2000; *H. klossii*: Tenaza 1975; *H. pileatus*: Brockelman and Srikosamatar 1984; *Nomascus concolor*: Zhenhe *et al.* 1989). However, most researchers reporting gibbon groups containing extra adults contacted the groups during surveys, making interpretation of the duration, nature, and importance of nonmonogamous grouping difficult. Accordingly, some researchers argue that 3-adult grouping is rare, and occurs primarily via retention of maturing offspring or as a response to

Table V Results of Bonferroni-corrected multiple comparisons of spatial and social variables among adult dyads

Group	Dyad	% Time <20 m apart		Mean inter-individual distance		% Time social grooming	
		Significance ^a	Direction ^b	Significance ^a	Direction ^b	Significance ^a	Direction ^b
A	AMI(m)-AMA(f)	NS	n/a	NS	n/a	$p=1.000$	NS
	AMI(m)-AMA(f)						
B	AMI(m)-AMU(m)	$p=.021^*$	+	$p=.002^*$	+	$p=.009^*$	+
	AMI(m)-AMA(f)						
	BMO(m)-BAM(f)						
	BMO(m)-BAR(m)						
C	BMO(m)-BAM(f)	$p<.001^*$	+	$p=.004^*$	+	$p=.052$	NS
	BMO(m)-BAR(m)						
	BMO(m)-CON(f)						
	BMO(m)-CKR(m)						
F	CGO(m)-CON(f)	$p=.845$	NS	$p=1.000$	NS	NS	n/a
	CGO(m)-CKR(m)						
	CGO(m)-CON(f)						
	CGO(m)-CKR(m)						
F	FRE(m)-FRI(f)	$p=.002^*$	+	$p=.002^*$	+	$p=.744$	NS
	FRE(m)-FRI(f)						
	FRE(m)-FRI(f)						
	FRE(m)-FRI(f)						
F	FRE(m)-FRI(f)	$p<.001^*$	+	$p=.005^*$	+	NS	n/a
	FRE(m)-FRI(f)						
F	FRE(m)-FRI(f)	$p=1.000$	NS	$p=1.000$	NS	NS	n/a
	FRE(m)-FRI(f)						

NS = ANOVA did not detect significant differences among all dyads in the group.

^a Results of Bonferroni-corrected multiple comparisons. Original ANOVA test statistics and p values are in the text. *Indicates a significant difference.

^b + Indicates results suggesting a closer spatial or social relationship between dyad 1 than dyad 2. Thus, for some variables, e.g. percentage of time spent <20 m apart, a significantly larger value is indicated by the + sign, whereas for others variables, e.g., mean interindividual distance, a significantly smaller value is indicated by the + sign.

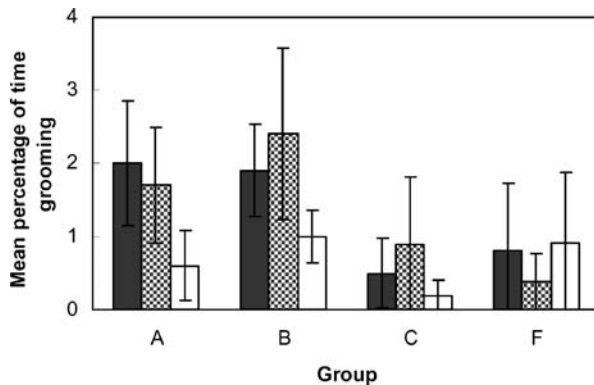


Fig. 4 Mean percentage of time that adult dyads spent in social grooming interactions (mean \pm 95% confidence intervals). Black bars represent the following dyads: male AMI and female AMA, male BMO and female BAM, male CGO and female CON, and male FRE and female FRI. Stippled bars represent dyads consisting of two adult males. White bars represent the following dyads: male AMU and female AMA, male BAR and female BAM, male CKR and female CON, and male FRA and female FRI.

anthropogenic habitat fragmentation (Chivers 2000). However, researchers have reported the formation of multimale white-handed gibbon groups via immigration of a second male and the long-term persistence of multimale groups in high-quality gibbon habitat (Brockelman *et al.* 1998), which suggests that multimale grouping may in some cases be best interpreted as a reproductive strategy. My findings confirm that relatively stable multimale grouping also occurs in siamangs, and that in at least some cases, siamang social polyandry is associated with low levels of aggression between male group members, regular affiliative social interactions between males, and sexual polyandry. The observations are consistent with the argument that siamangs display flexible grouping and mating patterns.

Role of Aggression in Multimale Siamang Groups

While data from relatively few groups are available, the apparent difference between rates of aggression between adult and subadult males at Kuala Lompat (Chivers 1974; Gittins and Raemaekers 1980) and between fully adult males at Way Canguk suggests that patterns of social interaction in groups containing 2 fully adult males may be less contentious than those in groups containing adult and younger males.

Table VI Copulations recorded in this study

Group	Male	Number of copulations
A	AMI	3
	AMU	1
B	BMO	13
	BAR	4
C	CGO	7
	CKR	6
F	FRE	4 ^a
	FRA	0

^a The figure includes 2 copulations involving adult male FRE and subadult female FUL.

Indeed, at Way Canguk 21 of 27 aggressive interactions in C involved large juvenile (or adolescent) male CBR and the 3 adults, which suggests that adults may preferentially direct aggression at smaller, younger males. Because males should promote unimale grouping should it be in their best interest to do so, the absence of frequent aggression between adult males suggests that the benefits of multimale grouping may have exceeded the costs for 1 or both males.

White-handed gibbons at Khao Yai compete aggressively for sexual access to the female (Sommer and Reichard 2000), but sexual aggression did not occur in Way Canguk siamangs. The absence of sexual aggression may indicate that aggression is not important in mediating mating competition between males. However, in African wild dogs, the intensity of aggression increased during the mating season (Creel and Creel 2002). There is no evidence that siamangs breed seasonally, and we observed copulations by both males in all 3 polyandrously mating groups on days when the pink and everted appearance of the female's genitalia suggested that she may have been near ovulation. However, none of the females' subsequent infants were conceived during the study, so it is possible that the low rates of aggression between males resulted from the low probability of conception during the study period.

Spatial Relationships Among Males at Way Canguk

While the nearest neighbor data, taken alone, might suggest that males BMO, CGO, and FRE actively avoid proximity with the second males, the complete spatial data set is more consistent with a group geometry involving close spatial cohesion between males BMO, CGO, and FRE and the group females, with the second males in B, C, and F maintaining looser cohesion with other adults. The pattern may result from avoidance of close proximity with other adults by the second males. However, in all 4 groups, both males spent most of their time ≤ 20 m from other adults, participated in all vocal choruses, and participated in social grooming interactions with other adults in their groups, which suggests that they were fully integrated into group life. Alternatively, males AMI, AMU, BMO, CGO, and FRE may have maintained particularly close spatial cohesion with adult females in their groups, perhaps as a form of mate-guarding, while males BAR, CKR, and FRA were more attracted to peripheral areas of the group's territory.

Attraction to peripheral areas may result from feeding competition, territorial concerns, or attraction to extragroup females. As the general pattern of spatial relationships in B, C, and F was similar in analyses excluding time spent feeding and there is no difference among adult mean daily path lengths, however, avoidance of feeding competition is not sufficient to explain the pattern of spatial relationships. Accordingly, it is reasonable to assume that differences in male ranging patterns may have resulted from differences in territorial behavior or patterns of mating investment.

How do Males Benefit from Multimale Grouping?

Tolerance between males may function as a form of parental investment. Though researchers did not report tolerance between purported fathers and sons at Kuala

Lompat, different ecological problems faced by males at Kuala Lompat and Way Canguk may lead to differences in the payoffs of male strategies. In saturated habitat, eviction of adult offspring may reduce male fitness if evicted offspring have little chance of obtaining a mate and territory. It is possible, then, that siamang males in saturated habitat may avoid directing aggression toward adult male offspring, permitting delayed dispersal. Indeed, researchers have reported parental tolerance and delayed dispersal in several primate species typically occurring in unimale unifemale groups (*Aotus azarai*: Fernandez-Duque and Huntington 2002; *Callicebus cupreus*: Bicca-Marquez *et al.* 2002; *C. moloch*: Mayeaux *et al.* 2002; *Hylobates lar*: Brockelman *et al.* 1998). Delayed dispersal of a natal male is the most parsimonious explanation for the observed pattern of spatial, social, and genetic data from F. It is clear that in A, B, and C neither adult male was the offspring of the group female, but a father-son relationship between males remains possible. Replacement of a group female may lead to step-families in which maturing males are offspring of the adult male, but are not genetic relatives of the group female (Palombit 1994b). Further, the observation that gibbon males often disperse relatively short distances from their natal groups (Bartlett 2003; Brockelman *et al.* 1998) raises the possibility that even in groups formed by immigration of a second male into a group already containing a male, there may be a close genetic relationship between males. If there is a genetic relationship between males, then kin selection should reduce the costs of polyandry.

Males may also have some incentive to accept polyandry when the second male is not a close relative. Brockelman *et al.* (1998) reported that at Khao Yai, most emigrating males formed new groups by replacing the adult male in an existing group. Given the difficulties that a male may face in obtaining a new mate and territory in saturated habitat, persistent aggression toward a determined male intruder may impose higher costs than acceptance of polyandry. This may be particularly true in cases in which the presence of a second male offers benefits to the first male.

The benefits of multimale grouping to male siamangs may include help with territorial defense (Brockelman *et al.* 1998) or help with infant care. Several researchers have described a relationship between helping behavior and polyandry in birds (Emlen 1982a, b), and mammals (Creel and Creel 2002; Goldizen *et al.* 1996; Tardif *et al.* 1993), and male care of infants is characteristic of siamangs (Chivers 1974; Chivers and Raemaekers 1980; Lappan 2005). However, though both males in most multimale groups at Way Canguk carried infants, infants of females that mated with multiple males actually received less direct male care than did the infant of a female in a unimale group did, or the female in F, which copulated with a single male (Lappan 2005).

However, there is some preliminary evidence that extra males may confer territorial advantages on their groups. Both males in all multimale groups at Way Canguk were active in territorial defense, and when intergroup interactions had a clear outcome, the larger group was more likely to win (Kinnaird *et al.* 2002). Larger siamang groups at Way Canguk also had higher mean numbers of figs in their home ranges and had significantly higher infant and juvenile survivorship than those of smaller groups (O'Brien *et al.* 2003), both of which suggest that group size may affect the ability to defend important food resources.

It is also possible that additional males provide assistance with mate guarding. Genetic research in a facultatively polyandrous bird species (white-browed scrubwren: *Sericornis frontalis*), demonstrated that dominant males in polyandrous groups suffered lower rates of paternity loss to extragroup males than males in unimale groups did (Whittingham *et al.* 1997). During several intergroup encounters at Way Canguk, a single male remained within close proximity of the female and immatures while the other male traveled 50–200 m away in pursuit of an intruding individual or group. In all 4 groups, each male occasionally remained >50 m from the remainder of the group for ≥ 1 h, which suggests that male help with mate guarding may free each male to spend more time pursuing extrapair copulation with neighboring females. Information about paternity and relatedness in and among multimale groups and more detailed information about male behavior during intergroup encounters would be useful in testing the ideas.

Acknowledgments The Leakey Foundation, Sigma Xi, the Fulbright Student Program, New York University, and Margaret and Herman Sokol provided funding for this research. The Indonesian Institute of Sciences (LIPI) granted permission to conduct research in Indonesia, and the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA) granted permission to conduct research at the Taman Nasional Bukit Barisan Selatan. I thank AMINEF, Universitas Indonesia, and the Wildlife Conservation Society-Indonesia Program for considerable logistical assistance in Indonesia. I thank students Abdul Roshyd and Martin Trisunu Wibowo, and technicians Janjiyanto, Sutarmin, and Tedy Prasetya Utama for their tireless assistance in the field, and Noviar Andayani, Simon Hedges, Margaret Kinnaird, Tim O'Brien, Nelly Paliama, Arnold Sitompul, and Martin Tyson for considerable logistical support. I thank Marina Cords, Roberto Delgado, Tony Di Fiore, Terry Harrison, Clifford Jolly, Tim O'Brien, Ryne Palombit, Larissa Swedell, and 2 anonymous reviewers for many helpful comments on earlier drafts of the article.

References

- Ahsan, M. F. (1995). Fighting between two females for a male in the Hoolock gibbon. *International Journal of Primatology*, 16, 731–737.
- Ahsan, M. F. (2000). Socio-ecology of the Hoolock gibbon (*Hylobates hoolock*) in two forests of Bangladesh. In *The Apes: Challenges for the 21st century*. Brookfield Zoo, May 10–13, 2000, Conference Proceedings. Chicago Zoological Park, Chicago, pp. 286–299.
- Bartlett, T. Q. (2003). Intragroup and intergroup social interactions in white-handed gibbons. *International Journal of Primatology*, 24, 239–259.
- Bicca-Marquez, J. C., Garber, P. A., & Azevedo-Lopes, M. A. O. (2002). Evidence of three resident adult male group members in a species of monogamous primate, the red titi monkey (*Callicebus cupreus*). *Mammalia*, 66, 138–142.
- Brockelman, W. Y., Reichard, U., Treesucon, U., & Raemaekers, J. (1998). Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, 42, 329–339.
- Brockelman, W. Y., & Srikosamatara, S. (1984). Maintenance and evolution of social structure in gibbons. In J. Prueschoft, D. J. Chivers, W. Y. Brockelman, & N. Creel (Eds.), *The lesser apes: Evolution, behaviour, and biology* (pp. 498–533). Edinburgh: Edinburgh University Press.
- Carpenter, C. R. (1940). A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comparative Psychology Monographs*, 16, 1–201.
- Chivers, D. J. (1974). The siamang in Malaya: a field study of a primate in tropical rain forest. In H. Kuhn, W. P. Luckett, C. R. Noback, A. H. Schultz, D. Stark, & F. S. Szalay (Eds.), *Contributions to primatology* (Vol. 4, pp. 1–335). Basel: Karger.
- Chivers, D. J. (2000). The swinging singing apes: fighting for food and family in far-east forests. In *The Apes: Challenges for the 21st Century*. Brookfield Zoo, May 10–13, 2000, Conference Proceedings. Chicago Zoological Park, Chicago, pp. 1–28.

- Chivers, D. J., & Raemaekers J. J. (1980). Long-term changes in behaviour. In D. J. Chivers (Ed.), *Malayan forest primates: Ten years' study in tropical rain forest* (pp. 209–258). New York: Plenum Press.
- Creel, S. R., & Creel, N. M. (2002). *The African dog: Behaviour, ecology and conservation*. Princeton: Princeton University Press.
- Emlen, S. T. (1982a). The evolution of helping I. an ecological constraints model. *American Naturalist*, 119, 29–39.
- Emlen, S. T. (1982b). The evolution of helping II. the role of behavioral conflict. *American Naturalist*, 119, 40–53.
- Fernandez-Duque, E., & Huntington, C. (2002). Disappearances of individuals from social groups have implications for understanding natal dispersal in monogamous owl monkeys (*Aotus azarai*). *American Journal of Primatology*, 57, 219–225.
- Fernandez-Duque, E., Mason, W. A., & Mendoza, S. P. (1997). Effects of duration of separation on responses to mates and strangers in the monogamous titi monkey (*Callicebus moloch*). *American Journal of Primatology*, 43, 225–237.
- Fuentes, A. (2000). Hylobatid communities: Changing views on pair bonding and social organization in hominoids. *Yearbook of Physical Anthropology*, 48, 86–88.
- Geissmann, T. (1999). Duet songs of the siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. *Behaviour*, 136, 1005–1039.
- Geissmann, T., & Orgeldinger, M. (2000). The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. *Animal Behavior*, 60, 805–809.
- Gittins, S. P. (1979). *The behaviour and ecology of the agile gibbon (Hylobates agilis)*. Ph.D. Dissertation, Cambridge University.
- Gittins, S. P. (1980). Territorial behavior in the agile gibbon. *International Journal of Primatology*, 1, 381–399.
- Gittins, S. P., & Raemaekers, J. J. (1980). Siamang, lar and agile gibbons. In D. J. Chivers (Ed.), *Malayan forest primates: Ten years' study in tropical rain forest* (pp. 63–105). New York: Plenum Press.
- Goldizen, A., Mendelson, J., van Vlaardingen, M., & Terborgh, J. (1996). Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *American Journal of Primatology*, 38, 57–83.
- Hinde, R. A. (1983). *Primate social relationships: An integrated approach*. London: Blackwell.
- Howell, N., Smejkal, C. B., Mackey, D. A., Chinnery, P. F., Turnbull, D. M., & Herrnstadt, C. (2003). The pedigree rate of sequence divergence in the human mitochondrial genome: There is a difference between phylogenetic and pedigree rates. *American Journal of Human Genetics*, 72, 659–667.
- Kinnaird, M. F., & O'Brien, T. G. (2005). Fast foods of the forest: The influence of figs on primates and hornbills across Wallace's line. In J. L. Dew & J. P. Boubli (Eds.), *Tropical fruits and frugivores*. New York: Springer.
- Kinnaird, M. F., O'Brien, T. G., Nurcahyo, A., & Prasetyaningrum, M. (2002). Inter-group interactions and the role of calling among siamangs. XIXth Congress of the International Primatological Society. August 4–9, 2002, Beijing China.
- Lappan, S. (2005). *Biparental care and male reproductive strategies in Siamangs (Symphalangus syndactylus) in Southern Sumatra, Indonesia*. Ph.D. Dissertation. New York University.
- Lappan, S. (2007). Patterns of dispersal in Sumatran Siamangs (*Symphalangus syndactylus*): Preliminary mtDNA evidence suggests more frequent male than female dispersal to adjacent groups. *American Journal of Primatology*, 69, 692–698.
- Leighton, D. R. (1987). Gibbons: Territoriality and monogamy. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 135–145). Chicago: University of Chicago Press.
- Mayeaux, D. J., Mason, W. A., & Mendoza, S. P. (2002). Developmental changes in responsiveness to parents and unfamiliar adults in a monogamous monkey (*Callicebus moloch*). *American Journal of Primatology*, 58, 71–89.
- Mitani, J. C. (1984). The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology*, 20, 265–269.
- Mitani, J. C. (1987). Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behavioral Ecology and Sociobiology*, 20, 227–265.
- O'Brien, T. G., Kinnaird, M. F., Nurcahyo, A., Iqbal, M., & Rusmanto, M. (2004). Abundance and distribution of sympatric gibbons in a threatened Sumatran rain forest. *International Journal of Primatology*, 25, 267–284.
- O'Brien, T. G., Kinnaird, M. F., Nurcahyo, A., Prasetyaningrum, M., & Iqbal, M. (2003). Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: *Hylobatidae*) in a Sumatran rainforest. *Animal Conservation*, 6, 115–121.

- Palombit, R. A. (1992). *Pair bonds and monogamy in wild Siamang (Hylobates syndactylus) and white-handed gibbon (Hylobates lar) in Northern Sumatra*. Ph.D. Dissertation, University of California, Davis.
- Palombit, R. A. (1993). Lethal territorial aggression in a white-handed gibbon. *American Journal of Primatology*, 31, 311–318.
- Palombit, R. A. (1994a). Extra-pair copulations in a monogamous ape. *Animal Behavior*, 47, 721–723.
- Palombit, R. A. (1994b). Dynamic pair bonds in hylobatids: Implications regarding monogamous social systems. *Behaviour*, 128, 65–101.
- Raemaekers, P. M., & Raemaekers J. J. (1985). Long range vocal interactions between groups of gibbons *Hylobates lar*. *Behaviour*, 95, 26–44.
- Reichard, U., & Sommer, V. (1997). Group encounters in wild gibbons (*Hylobates lar*): Agonism, affiliation, and the concept of infanticide. *Behaviour*, 134, 1135–1174.
- Schaffner, C. M., & French, J. A. (2004). Behavioral and endocrine responses in male marmosets to the establishment of multimale breeding groups: evidence for non-monopolizing facultative polyandry. *International Journal of Primatology*, 25, 709–732.
- Siddiqi, N. A. (1986). Gibbons (*Hylobates hoolock*) in the West Bhanugach Reserved Forest of Sylhet District, Bangladesh. *Tigerpaper* 8: 29–31.
- Sommer, V., & Reichard, U. (2000). Rethinking monogamy: The gibbon case. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 159–168). Cambridge, UK: Cambridge University Press.
- Tardif, S., Harrison, M., & Simek, M. (1993). Communal infant care in marmosets and tamarins: relation to energetics, ecology, and social organization. In A. B. Rylands (Ed.), *Marmoset and tamarins. Systematics, behaviour and ecology* (pp. 220–234). Oxford: Oxford University Press.
- Tenaza, R. R. (1975). Territory and monogamy among Kloss' gibbons (*Hylobates klossii*) in Siberut island, Indonesia. *Folia Primatologica*, 24, 60–68.
- Tilson, R. L. (1981). Family formation strategies of Kloss's gibbons. *Folia Primatologica*, 35, 259–287.
- West, K. (1981). *The behavior and ecology of the Siamang in Sumatra*. M.A. Thesis, University of California, Davis.
- Whittingham, L. A., Dunn, P. O., & Magrath, R. D. (1997). Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren. *Behavioral Ecology and Sociobiology*, 40, 261–270.
- Zhenhe, L., Zhang, Y., Jiang, H., & Southwick, C. (1989). Population structure of *Hylobates concolor* in Bawanglin nature reserve, Hainan, China. *American Journal of Primatology*, 119, 247–254.